
SYSTEMATICS OF THE SOUTH AMERICAN *HYPOCHAERIS* *SESSILIFLORA* COMPLEX (ASTERACEAE, CICHORIEAE)¹

Estrella Urtubey,² *Tod F. Stuessy*,³ and
*Karin Tremetsberger*⁴

ABSTRACT

The *Hypochaeris sessiliflora* complex (Asteraceae, Cichorieae) consists of nine species of the genus from South America (all in section *Achyrophorus* Scop.) that have sessile or nearly sessile flowering heads surrounded by a rosette of leaves. They occur at 1430–5100 m in elevation along the Andean chain from Venezuela to Chile and Argentina. Two species, *H. sessiliflora* Kunth and *H. meyeniana* (Walp.) Benth. & Hook. f. ex Griseb., are extremely polymorphic, and they vary conspicuously in the shape of the external phyllaries and presence or absence of different types of trichomes. They have the widest distributions (Venezuela to central Peru, and Peru to northern Chile and northwestern Argentina, respectively), they flower throughout the year, and they also are primarily associated with dry and sunny habitats. *Hypochaeris meyeniana* is characterized by retrorsely pinnatifid leaves (rarely lobate) and slightly narrower cypselar apices. *Hypochaeris hohenackeri* (Sch. Bip.) Domke and *H. taraxacoides* Ball are glabrous, whereas *H. acaulis* (J. Rémy) Britton has scattered shaggy trichomes on the leaves; all three occur in humid places, such as seeps or bogs. *Hypochaeris eriolaena* (Sch. Bip.) Reiche and *H. mucida* Domke are pubescent, with long whiplike trichomes on leaves and phyllaries, giving a niveous-tomentose appearance. *Hypochaeris echegarayi* Hieron. (white corollas) and *H. eremophila* Cabrera (yellow corollas) are two related species with shaggy trichomes on the abaxial surfaces of the phyllaries, both with considerable ecological tolerance, that grow in dry as well as humid sites. Morphological cladistic analyses suggest a hypothesis of relationships within the complex. Surprisingly, *H. acaulis* from Chile and Argentina, although fitting morphologically within the *H. sessiliflora* complex, based on amplified fragment length polymorphism (AFLP) data, clearly does not seem to belong to this group. Instead, the species ties to *H. palustris* (Phil.) De Wild. and *H. tenuifolia* (Hook. & Arn.) Griseb., also from the southern Andes. The acaulescent habit of *H. acaulis* seems best interpreted as a parallel adaptation to survival at high elevations.

RESUMEN

El complejo *Hypochaeris sessiliflora* comprende nueve especies de Sudamérica (sección *Achyrophorus* Scop.) con cabezuelas sésiles o cortamente pedunculadas y con una roseta de hojas basales. Habitan entre los 1430–5100 m a lo largo de los Andes desde Venezuela hasta el centro de Chile y el centro oeste de Argentina. Dos especies, *H. sessiliflora* Kunth e *H. meyeniana* (Walp.) Benth. & Hook. f. ex Griseb., son extremadamente polimórficas (forma de los filarios, hojas e indumento) y presentan una amplia distribución, desde Venezuela al centro de Perú, y desde Perú al norte de Chile y noroeste de Argentina, respectivamente; principalmente crecen en ambientes secos y soleados, y florecen todo el año. *Hypochaeris meyeniana* se caracteriza por las hojas pinnatífidas y retrorsas (raro lobadas) y los aquenios ligeramente adelgazados en el ápice. *Hypochaeris hohenackeri* (Sch. Bip.) Domke e *H. taraxacoides* Ball son glabras, mientras que *H. acaulis* (J. Rémy) Britton tiene hojas hispídas; estas tres especies están asociadas a ambientes húmedos (e.g., vegas y mallines). *Hypochaeris eriolaena* (Sch. Bip.) Reiche e *H. mucida* Domke son niveo-tomentosas. *Hypochaeris echegarayi* Hieron. (corolas blancas) e *H. eremophila* Cabrera (corolas amarillas) son especies afines con pubescencia hispídas, comúnmente con cabezuelas pedunculadas y con considerable tolerancia ecológica, creciendo en ambientes secos o húmedos. La hipótesis del análisis cladístico morfológico y los recientes estudios moleculares muestran al complejo *H. sessiliflora* monofilético mientras que la hipótesis basada en datos moleculares excluye a *H. acaulis* del complejo *H. sessiliflora*, donde el hábito acaule es considerado una adaptación paralela como respuesta a la sobrevivencia en la alta montaña.

Key words: *Achyrophorus*, Asteraceae, Cichorieae, *Hypochaeris*, South America.

¹ We express thanks to John McNeill and Werner Greuter for help with the nomenclature of *Hypochaeris taraxacoides*; A. Migoya and M. Theiller for illustrations of the species and H. Calvetti for help with maps; the curators of BM, CONC, K, LP, LPB, M, MCNS, MO, NY, OS, P, SGO, SI, UC, US, W, and WU for loans or permission to consult herbarium material; M. Muñoz (SGO) and L. Willemse (L) for digital images of the types of *Distoecha taraxacoides* and *H. ornata* and *H. parvifolia*, respectively; F. Felbe and F. Jacquemoud for information on types at NEU and G, respectively; V. Noble, N. Hind, and S. Barrier for their assistance during visits to BM, K, and P; S. E. Freire and D. Giuliano for valuable comments on the manuscript; A. Luck for editorial help with various drafts of the manuscript; and financial support from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PEI and PIP6510), Myndel Botanica Foundation, a small grant from the University of Vienna, and the Austrian National Science Foundation (FWF, grant numbers P15225-BIO and P18446-B03).

² Instituto de Botánica Darwinion, Labardén 200, San Isidro, B1642HYD, Casilla de Correo 22, Buenos Aires, Argentina. eurtubey@darwin.edu.ar.

³ Department of Systematic and Evolutionary Botany, Faculty Center Biodiversity, University of Vienna, Rennweg 14, A-1030 Vienna, Austria. tod.stuessy@univie.ac.at.

⁴ Institute of Botany, Department of Integrative Biology and Biodiversity Research, University of Natural Resources and Applied Life Sciences, Vienna, Gregor-Mendel-Straße 33, A-1180 Vienna, Austria. karin.tremetsberger@boku.ac.at.

doi: 10.3417/2006136

Hypochaeris L. consists of about 60 species of annual or perennial herbs in Asteraceae, tribe Cichorieae Lam. & DC., subtribe Hypochaeridinae Less., which are characterized by paleae on receptacles, a plumose pappus, and style branches papillose to well below the bifurcation (Fig. 1A–C). The genus has a disjunct distribution, with ca. 12 species scattered in the Mediterranean region, two in Central Europe, one in Asia, and the remainder (some 40 to 50 species) in South America. Hoffmann (1893) reduced the 10 sections of Bentham and Hooker (1873) to five, based on the number of rows of pappus bristles, shapes of heads, arrangements of phyllaries, and shapes of the cypselae. One of these sections, *Achyrophorus* Scop., is characterized primarily by having a uniseriate pappus; all species from South America fall into this group.

Previous evolutionary studies have been completed on species of *Hypochaeris* from South America. Chromosome counts from many species and populations have revealed most members of *Hypochaeris* to be diploid, with some infraspecific polyploidy, and with some species uniformly tetraploid (Baeza et al., 2000; Weiss et al., 2003; Weiss-Schneeweiss et al., 2007, 2008). Although all diploids uniformly have $2n = 8$, small karyotypic differences allow hypotheses regarding modes of cytogenetic evolution (Weiss-Schneeweiss et al., 2003). Sequences of nuclear ribosomal ITS (nrITS) and chloroplast DNA have revealed that the South American species are monophyletic and that they are closest to *H. angustifolia* Maire from Morocco (Samuel et al., 2003; Tremetsberger et al., 2005). Sequence variation within species from South America is minimal, and no clades can be recognized with high levels of confidence. Amplified fragment length polymorphism (AFLP) studies have helped reveal phyletic assemblages within the South American taxa (Tremetsberger et al., 2006), as well as indicate phylogeographic trends at the populational level in *H. acaulis* (J. Rémy) Britton, *H. palustris* (Phil.) De Willd., and *H. tenuifolia* (Hook. & Arn.) Griseb. (Tremetsberger et al., 2003a, b; Muellner et al., 2005).

Among the South American taxa, a morphologically distinctive group is formed by species that have single sessile or nearly sessile capitula nestled among a rosette of basal leaves, the so-called *Hypochaeris sessiliflora* complex. These taxa occur from Venezuela south into Chile and Argentina and occur at 1430–5100 m, usually in dry habitats or in seeps within these high Andean regions. This paper focuses on this complex as a beginning for understanding detailed morphological relationships within the South American species of *Hypochaeris*. A revision of all taxa is included plus a morphological cladistic analysis.

CLADISTIC ANALYSIS

MATERIALS AND METHODS

Morphological characters and states were obtained primarily from study of herbarium material from BM, CONC, K, LP, LPB, M, MCNS, MO, NY, OS, P, SGO, SI, UC, US, W, and WU, plus our additional collections and field observations. Trichomes and stomatal types and terminology are used according to Metcalfe and Chalk (1950, 1979), Uphof (1962), and Harris and Harris (1994). For study of vascularization of corollas and cypselae, the clearing and staining method of Fuchs (1963) was used. Information regarding color, habitat, and phenology of plants was taken from specimen labels, the literature, and our field observations. Chromosome numbers were obtained from the reviews of Weiss et al. (2003) and Weiss-Schneeweiss et al. (2007, 2008).

The ingroup consisted of all nine South American species of the *Hypochaeris sessiliflora* complex: *H. acaulis*, *H. echegarayi* Hieron., *H. eremophila* Cabrera, *H. eriolaena* (Sch. Bip.) Reiche, *H. hohenackeri* (Sch. Bip.) Domke, *H. meyeniana* (Walp.) Benth. & Hook. f. ex Griseb., *H. mucida* Domke, *H. sessiliflora* Kunth, and *H. taraxacoides* Ball. We included five additional South American species of *Hypochaeris* to serve as outgroup. These species were selected to represent morphological diversity within *Hypochaeris* on the continent, two of which (*H. hookeri* Phil. and *H. caespitosa* Cabrera) are believed to be close relatives of the *H. sessiliflora* complex. *Hypochaeris hookeri* is closely related morphologically to the complex (especially in its acaulescent habit). Its leaves are long, linear, and erect, the peduncle is shorter than the leaves, and the paleae have trichomes on the adaxial surface; it is distributed in central-western Argentina and central-eastern Chile. *Hypochaeris caespitosa* is also an acaulescent herb, the peduncle is longer than the leaves, and it inhabits the mountain ranges of central Argentina. We also examined three caulescent species, *H. argentina* Cabrera of central Argentina, and *H. chillensis* (Kunth) Hieron. and *H. elata* (Wedd.) Benth. & Hook. f. ex Griseb. from Peru, south into Argentina.

To provide a context for selection of characters and states in the cladistic analysis, and to better clarify the character data used in the descriptions of each taxon, a sketch of the morphology of the complex follows here (see also Fig. 1). All nine species of the *Hypochaeris sessiliflora* complex are dwarf perennial herbs, from only 1 cm (*H. mucida*) to 13 cm (in *H. sessiliflora*) tall. They are acaulescent plants with thick rhizomes and rosette leaves. The capitula are always solitary, and they can be sessile or shortly

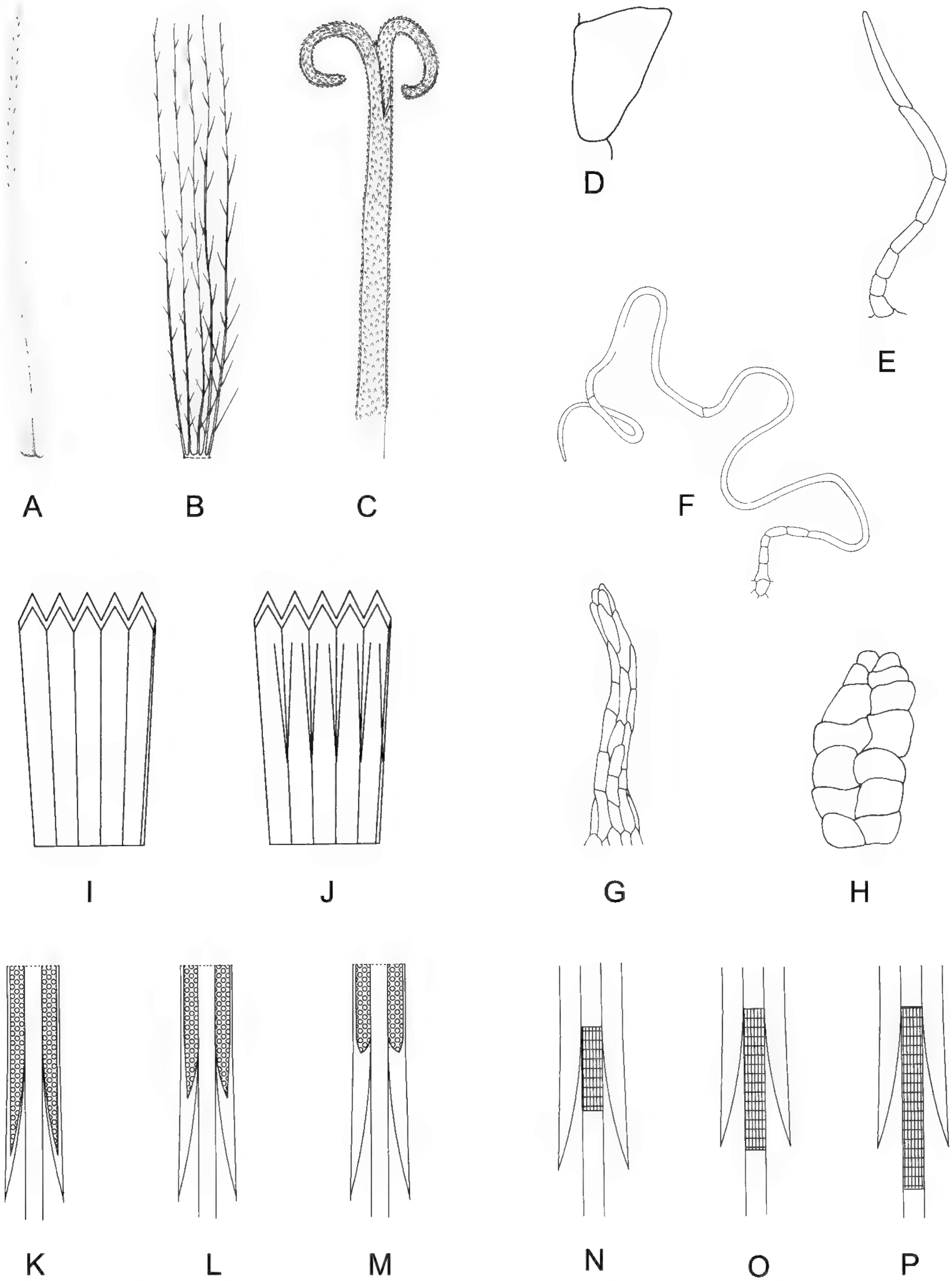


Figure 1. Selected morphological features of taxonomic efficacy in the *Hypochaeris sessiliflora* complex. —A. Palea. —B. Plumose pappus bristles. —C. Papillose style. D–H. Trichomes. —D. Papillate. —E. Conical (many-celled). —F. Whip. —G. Shaggy. —H. Glandular. I, J. Corolla vascularization. —I. Type 1. —J. Type 2. K–M. Anther tails. —K. Type 1. —L. Type 2. —M. Type 3. N–P. Basal appendages. —N. Type 1. —O. Type 2. —P. Type 3.

pedunculate (never longer than the leaves). The leaves are entire or pinnatisect, the leaf base is attenuate in a long petiole and tomentose, and the blades are commonly lanceolate or linear to elliptic. The leaf margin is entire or dentate. The epidermal cells are lightly undulate, and the stomata are anomocytic.

The involucre is commonly campanulate, campanulate-cylindrical (*Hypochaeris eremophila*), or cylindrical (*H. taraxacoides*), and sometimes hemispheric (*H. acaulis*, *H. meyeniana*, and *H. sessiliflora*). The phyllaries are in three to six series. The outer ones are lanceolate to broadly ovate, often becoming gradually lighter toward the hyaline margin. The maximum expression of this character state occurs in some populations of *H. sessiliflora* in which the apical margin is broadly expanded, called “cucullate” (hooded), and it can be entire or divided. The phyllaries are either glabrous or ciliate, sometimes lanuginous (whip trichomes) and/or setaceous (shaggy trichomes). The adaxial side of the paleae is glabrous.

The corolla is of typical Lactuceae-type, i.e., ligulate and 5-lobed, with epidermal cells lightly undulate and with epicuticular plated waxes (very conspicuous in *Hypochaeris mucida*), and it has short trichomes on the middle third. The vascularization of corollas is characterized by the adjacent marginal bundles united and fused at the apex of their lobes, and there are two different types of vascularization. The most common pattern has five marginal bundles united at the apex of the lobes (type 1, Fig. 1I); the other type comprises the same number of bundles, but these are repeatedly divided in the throat and ligule of the corolla (type 2, Fig. 1J). The color of the corolla varies: white in *H. echegarayi* and *H. taraxacoides*; yellow in *H. acaulis*, *H. eremophila*, and *H. hohenackeri*; or white, yellow, or orange in *H. eriolaena* and *H. sessiliflora*. Some plants with pink corollas in *H. hohenackeri* and *H. sessiliflora* have been collected. We have no information about the corolla color of *H. mucida*, because the available specimens are too faded, none of the herbarium labels mention the color, and we have not collected the taxon.

The five stamens have short anther tails, with basal appendages with pollen sacs extending almost to the end (1/2 to 3/4, Fig. 1K), into the middle or less (1/4 to 1/2, Fig. 1L), or basal appendages with only sterile cells (Fig. 1M). The antheropodium consists of epidermal cells that are axially elongated with thickened and lignified walls, and it can be shorter than, the same length as, or longer than the basal appendages (Fig. 1N–P).

The cypselae are commonly erostrate or narrowed toward the apex; in *Hypochaeris acaulis* they are rostrate. The cypselae are usually 5-ribbed (some-

times inconspicuous), and the surface is smooth or scaly and striate.

Five types of trichomes are present, three being uniseriate: (1) papilla-like (Fig. 1D), a small unicellular epidermal cell thickened at the apex, being present on lobes of the corolla; (2) conical (Fig. 1E), 2- to many-celled, e.g., on the margins of the palea or pappus bristles (2-celled), or comprising the cilia of the phyllaries (2- to many-celled); and (3) whip (Fig. 1F), many-celled, with a very long apical cell, present on the surfaces of leaves and phyllaries of *Hypochaeris eriolaena* and *H. mucida*. Other types of trichomes are multiseriate: (1) shaggy (Fig. 1G), many-celled, ending in one to few cells, forming a setaceous indumentum (these trichomes are often brown or red, i.e., on phyllaries of *H. echegarayi*, *H. eremophila*, and *H. sessiliflora*); and (2) biseriate-glandular (Fig. 1H), present on the leaf surface of some populations of *H. sessiliflora*. We have used the term glabrous when trichomes are relatively few or totally absent.

From this spectrum of morphological variation, 16 morphological characters (five vegetative and 11 floral) were selected for assessing evolutionary relationships among the taxa. These are listed in Appendix 1, and selected features are highlighted in Figure 1. Autapomorphic characters were not included in the analysis. The data matrix of the 14 species and 16 characters is given in Appendix 2; vouchers are listed in Appendix 3. A complete listing of specimens cited in this study is presented in Appendix 4. Polymorphisms represent nearly 20% of the data. Character 2 was uninformative within the complex, but it was included because it is important for circumscribing all the caulescent species of *Hypochaeris*.

Phylogenetic analyses were performed with PeeWee 3.0 (Goloboff, 1998). Initial PeeWee runs were conducted using sequence commands holding 10000: rseed 0, hold/40, poly—, amb—; mult*500; fit* — fit rescaled. All characters were weighted equally and character states were treated as unordered. Jackknife support values for nodes were calculated with 1000 replicates, two search replicates (mult*2), and two starting trees per replication (hold/2). Character distributions were studied and strict consensus trees were calculated using Winclada (Nixon, 1999).

RESULTS

The analyses resulted in one most parsimonious tree of 40 steps, with fit — 110 and fit* — 57%; synapomorphies and homoplasies are mapped onto the phylogeny (Fig. 2). All species except *Hypochaeris argentina* are supported by the presence of type 1

corolla vascularization (character 11, state 1). The pair *H. chillensis*–*H. elata* is supported by corollas with the same length as the involucre (character 10, state 1) and a jackknife value of 64. *Hypochaeris caespitosa* and the rest of the species are supported by possessing linear-lanceolate leaf laminae (character 3, state 4), whip trichomes on the abaxial surface of the phyllaries (character 9, state 1), and smooth cypselar walls (character 15, state 1). *Hypochaeris hookeri* is the sister species of the ingroup, a clade supported by acaulescent plants or plants with shortly pedunculate heads (character 1, state 1) and jackknife support of 56. The *H. sessiliflora* complex is supported as a monophyletic clade by glabrous phyllaries and paleae (character 9, state 3 and character 16, state 1) and with jackknife support of 59, and *H. sessiliflora* is the basal species. The clade of the remaining species is supported by linear leaves (character 3, state 1). *Hypochaeris hohenackeri* through *H. acaulis* are supported by lanceolate phyllaries (character 8, state 1). The clade of *H. mucida* and the rest of the species is supported by sessile heads (character 7, state 1). The remaining three groups are supported primarily by homoplasies, the first homoplasy being a reversal (scaly cypselar wall, character 15, state 0), followed by a parallelism (divided leaves, character 4, state 2). The unresolved complex consisting of *H. meyeniana*, *H. echegarayi*, and *H. eremophila* is supported by a reversal (lanceolate leaves, character 3, state 0) and one synapomorphy (shaggy phyllaries, character 9, state 2).

DISCUSSION

Hypochaeris hookeri appears as the sister species of the ingroup. Future studies, including the rest of the South American species, must evaluate whether *H. hookeri* should properly belong to the *H. sessiliflora* complex or not. The results tentatively support monophyly of the *H. sessiliflora* complex, but for a critical morphological assessment of this question, a cladistic analysis of all South American taxa must be completed.

The basic structure of relationships (Fig. 2) makes considerable sense. *Hypochaeris sessiliflora* is a large, acaulescent herb that contains conspicuous morphological variation (Fig. 3) and has a broad range in the northern Andes (Fig. 4A). *Hypochaeris taraxacoides* and *H. hohenackeri* are very close relatives morphologically (cf. Figs. 5, 6) and are found in similar seeps above 2600 m in the central Andes (Fig. 4B, squares and circles). Their evolutionary history must be closely entwined.

Hypochaeris mucida and *H. eriolaena* are both very tomentose with sessile heads (Figs. 7, 8). They are easily distinguished from each other in features of the

involucre, corolla vascularization, and cypselar wall. *Hypochaeris mucida* is a dwarf herb, up to only 1.5 cm tall, densely pubescent, with shaggy and whip trichomes on the backs of the phyllaries and leaves, and growing above 4500 m in grassy steppes associated with *Pycnophyllum* J. Rémy (Caryophyllaceae Juss.) in southeastern Peru and northwestern Bolivia on the eastern side of Lake Titicaca (Fig. 4B, triangles). *Hypochaeris eriolaena* has whip trichomes on the backs of the phyllaries and leaves (or glabrous), and it inhabits dry places (between 2200 and 5100 m) from Peru to Bolivia (Fig. 4C, squares).

The other rosette taxa with divided leaves, *Hypochaeris meyeniana*, *H. echegarayi*, and *H. eremophila*, are closely related. Morphologically, the last two are similar (Figs. 9, 10), both with relatively short peduncles, very divided leaves, phyllaries with long trichomes on the midribs (Figs. 10C, D; 11C–E), and plumose pappus bristles. They have different and consistent floral colors: white versus yellow, respectively. They are also both found in the junction between southern Peru, southwestern Bolivia, and northwestern Argentina. It is very likely that these two taxa share a common origin. *Hypochaeris meyeniana* is similar to the other two, but its heads are subsessile, leaves less divided, phyllaries nearly glabrous, and pappus bristles with very short side trichomes (Fig. 11).

Hypochaeris acaulis, which occurs only in the southern Andes (Figs. 12, 13), is geographically far removed from the other taxa of the *H. sessiliflora* complex. Although morphologically *H. acaulis* fits comfortably within this complex (it can be differentiated from the other species of this complex by its broader phyllaries and rostrate cypselae; Fig. 12; see also key), recent AFLP data do not support this inclusion. Based on a broad sampling of taxa of *Hypochaeris* within South America (but not including *H. mucida* due to lack of material), Tremetsberger et al. (2006) have shown that *H. acaulis* does not at all relate to the *H. sessiliflora* complex, but instead to *H. palustris* and *H. tenuifolia*, which are also found at high elevations along volcanoes of the southern Andes in Chile and Argentina (Tremetsberger et al., 2003a, b; Muellner et al., 2005). This makes sense geographically. *Hypochaeris acaulis* appears to represent a case of extreme morphological parallelism as adaptation for survival against the harsh environment (especially low temperatures and wind). *Hypochaeris acaulis* is included here for convenience; it will be separated in a future comprehensive treatment of the entire South American complex of the genus.

Considering the classical biogeographic division of the Andes into three portions (Morrain, 1984; Taylor, 1991), the northern Andes (10°N to 3°S), central

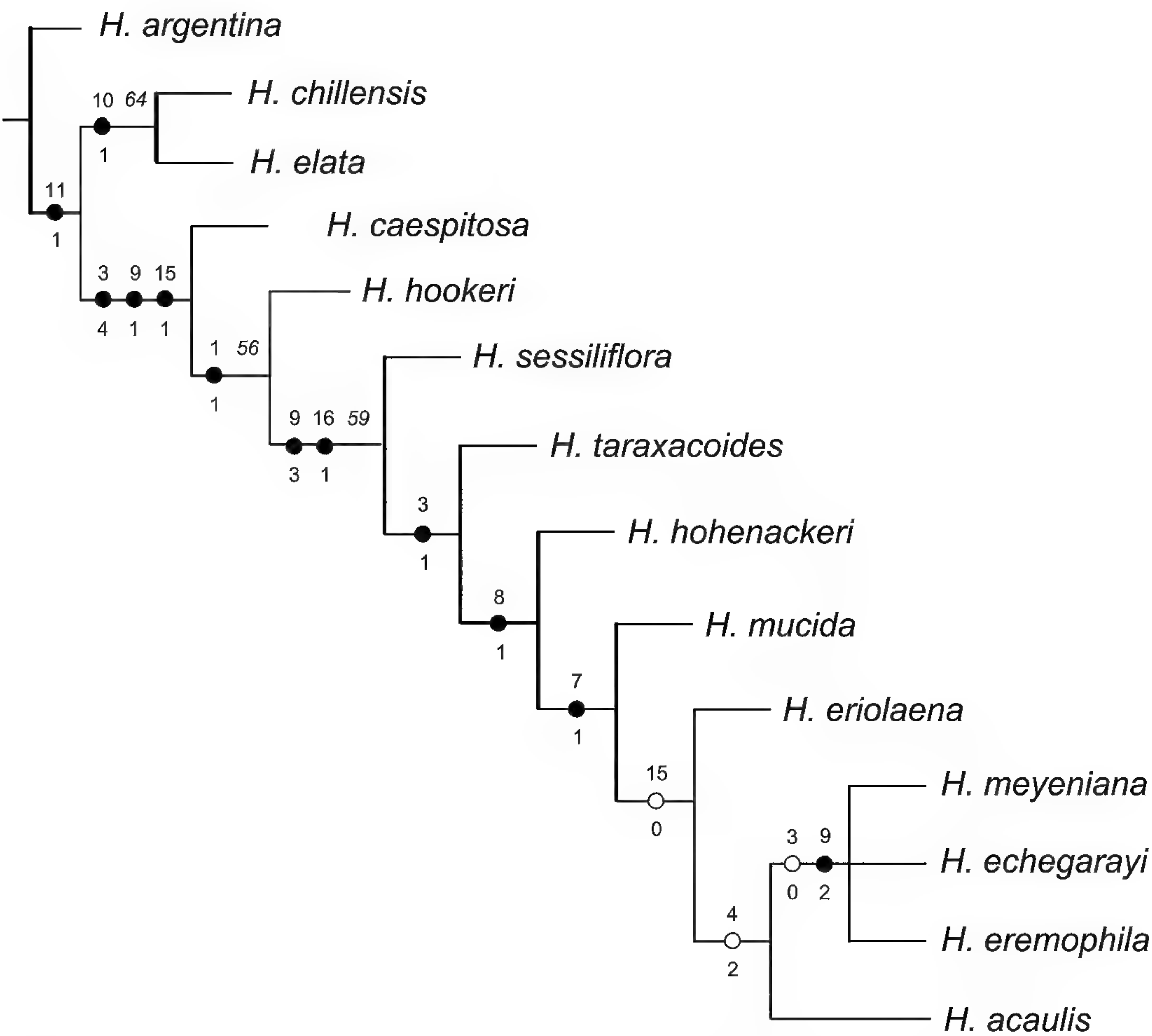


Figure 2. Most parsimonious tree of 40 steps (fit = 110; fit* = 57%), showing all characters (numbers above line) and states (numbers below line; see Appendix 1) for clades. Closed circles indicate synapomorphies; open circles indicate homoplasies (parallelisms or reversals). The numbers in italics are jackknife support values greater than 50% taken from a strict consensus tree.

Andes (3°S to 18°S), and southern Andes (18°S to 54°S), only *H. sessiliflora* is present in the northern Andes (Fig. 4A). *Hypochaeris acaulis* is the only taxon in the southern Andes; as discussed above, it appears to have had an independent evolutionary history. Most of the species of the complex occur in the central Andes; the major evolutionary and biogeographic differentiation must have occurred in this general region. Exactly what the mechanisms of speciation and biogeography have been in this subgroup remain to be determined; they likely have involved dispersal throughout the zone, isolation due to diverse topography, adaptation to local ecologic conditions, and eventual local speciation. Suspected hybridization between *H. echegarayi* and *H. meyeniana* (pers. field obs.) in western Bolivia emphasizes the evolutionary

closeness of this group and perhaps also its recent evolutionary origins.

TAXONOMIC TREATMENT

Hypochaeris L., Sp. Pl. 2: 810. 1753. TYPE: *Hypochaeris glabra* L.

The genus *Hypochaeris* is characterized by the presence of latex, ligulate corollas, receptacular paleae, and a plumose pappus. It comprises approximately 60 species with an important center of diversification in South America (where more than 2/3 of the species occur). The rest of the taxa inhabit the Old World and Asia. All South American species fall under section *Achyrophorus*, characterized by the presence of a uniseriate pappus.

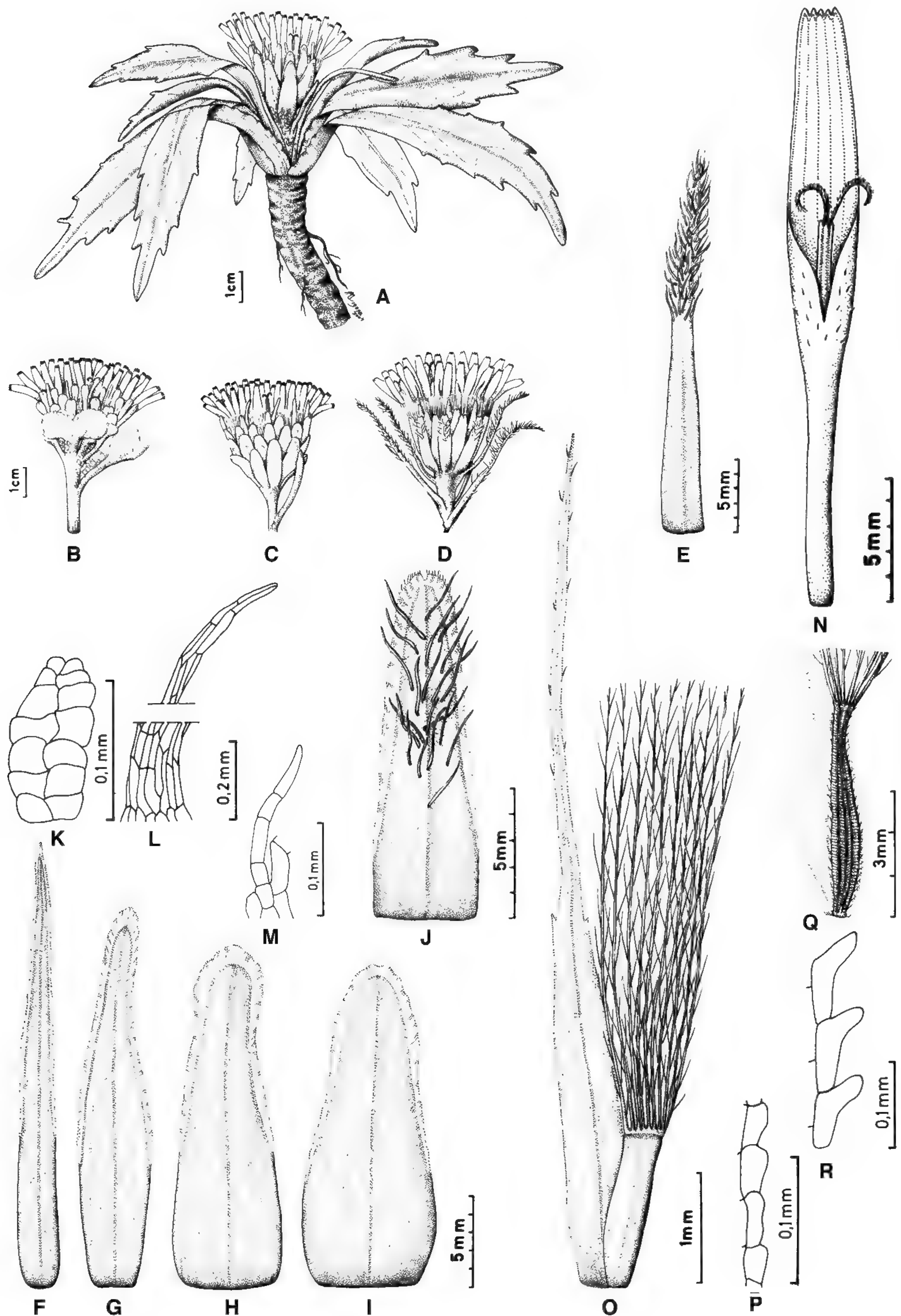


Figure 3. *Hypochaeris sessiliflora*. —A. Habit. —B–D. Variation in capitula and phyllaries. —E. Setaceous bract. —F–J. Phyllaries. K–M. Trichomes occurring on some phyllaries. —K. Glandular trichomes. —L. Shaggy trichomes. —M. Conical trichomes. —N. Corolla with anthers and style. —O. Palea, cypselae, and pappus. —P. Smooth achenial wall. —Q, R. Scaly cypselar wall. A, C, F–I, N–P from Cuatrecasas et al. 25599 (US); B from Stuessy et al. 18538 (LP); and D, E, J–M, Q, R from Plowman 1955 (US).

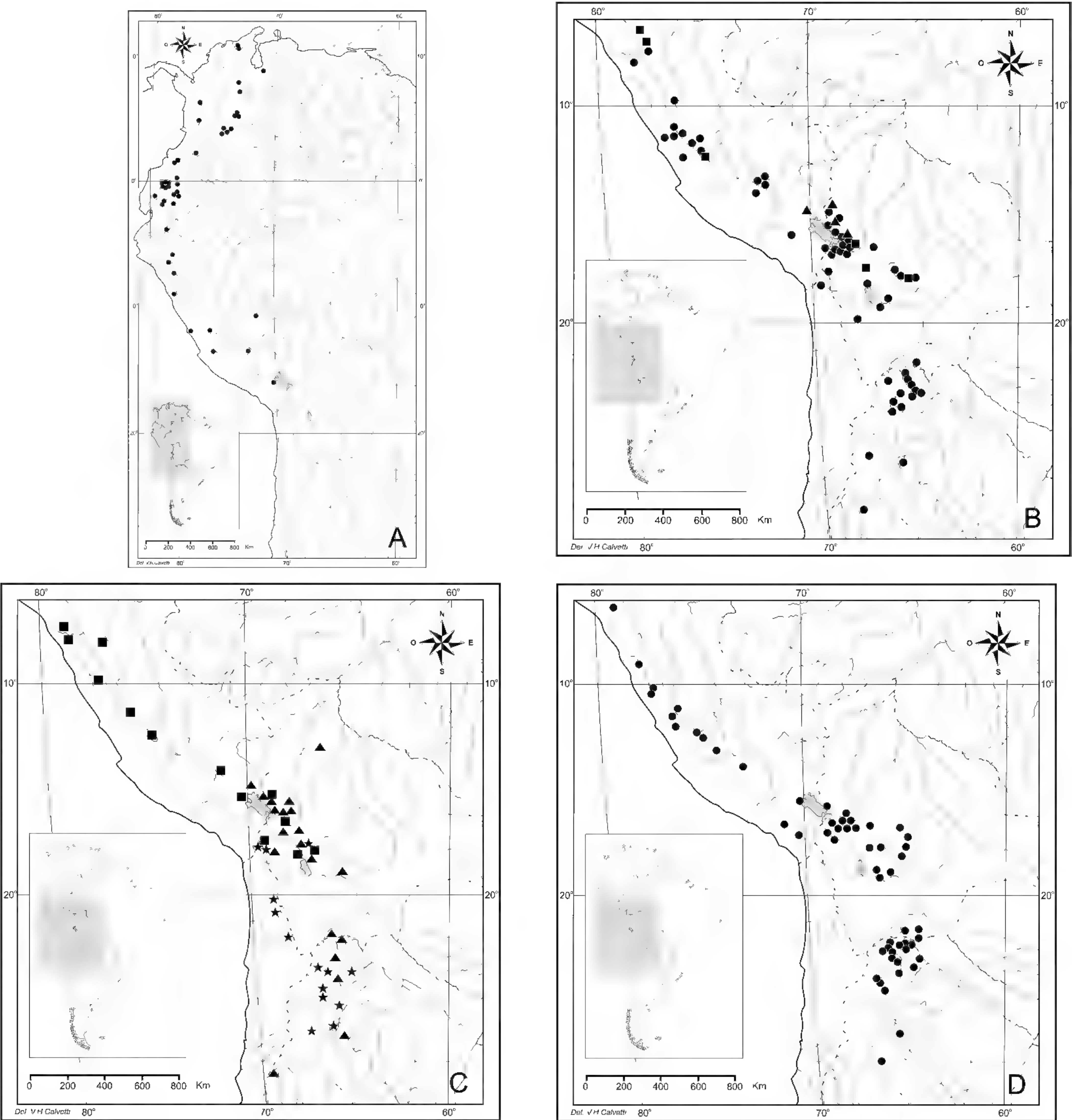


Figure 4. —A. Distribution of *Hypochaeris sessiliflora* in the northern and central Andes. —B. Distribution in the central and northern Andes of *H. hohenackeri* (■), *H. mucida* (▲), and *H. taraxacoides* (●). —C. Distribution in the central Andes of *H. echegarayi* (▲), *H. eremophila* (★), and *H. eriolaena* (■). —D. Distribution of *H. meyeniana* in the central Andes.

The *Hypochaeris sessiliflora* complex comprises nine South American species of dwarf (1–13 cm tall), perennial, acaulescent herbs, with solitary capitula that are sessile or pedunculate (shorter than the

leaves), which inhabit dry and humid places along the Andean mountains, from southern Venezuela to central-eastern Chile and northwestern Argentina, between 1430 and 5100 m.

KEY TO SPECIES OF THE *HYPOCHAEERIS SESSILIFLORA* COMPLEX

- 1a. Outer phyllaries broadly ovate (as wide as long); cypselae rostrate, proximally scaly 9. *H. acaulis*
- 1b. Outer phyllaries usually longer than wide; cypselae erostrate or narrower near apices, scaly or smooth.
 - 2a. Involucre cylindric; corollas white 2. *H. taraxacoides*
 - 2b. Involucre campanulate-cylindric, campanulate to hemispheric, corollas yellow (white in *H. echegarayi*, sometimes white in *H. sessiliflora*).
 - 3a. Plants to 1.5 cm tall; phyllaries with both whip and shaggy trichomes 4. *H. mucida*
 - 3b. Plants 3–13 cm tall; phyllaries glabrous or with only one type of trichome.
 - 4a. Leaves undivided (margins entire or dentate).

- 5a. Outer phyllaries lanuginous (whip trichomes) toward the apex 5. *H. eriolaena*
- 5b. Outer phyllaries glabrous or setulose (shaggy trichomes).
 - 6a. Leaves linear-lanceolate or elliptic-lanceolate 1. *H. sessiliflora*
 - 6b. Leaves oblong 3. *H. hohenackeri*
- 4b. Leaves pinnatipartite to pinnatisect.
 - 7a. Corollas white 7. *H. echegarayi*
 - 7b. Corollas yellow.
 - 8a. Heads usually sessile; involucre campanulate 6. *H. meyeniana*
 - 8b. Heads usually pedunculate; involucre cylindric-campanulate 8. *H. eremophila*

1. *Hypochaeris sessiliflora* Kunth, Nov. Gen. Sp. [HBK], folio ed. 4: 2. 1818, quarto ed. 4: 2. 1820. *Oreophila sessiliflora* (Kunth) D. Don, Trans. Linn. Soc. London 16: 178. 1830. *Achyrophorus sessiliflorus* (Kunth) DC., Prodr. (DC.) 7: 95. 1838. TYPE: Ecuador. Prov. Pichincha: "crescit in alta convalli Quitensi, juxta montem ignivomum Pichincha, alt. 1500 hex." [ca. 3000 m], 14 Apr. 1802 [Sandwith, 1926], *F. W. H. A. von Humboldt & A. J. G. Bonpland s.n.* (holotype, P!, P photo MO!). Figure 3.

Hypochaeris sonchoides Kunth, Nov. Gen. Sp. [HBK], quarto ed. 4: 2. 1818, quarto ed. 4: 2. 1820. *Achyrophorus sonchoides* (Kunth) DC., Prodr. (DC.) 7: 95. 1838. *Achyrophorus quitensis* Sch. Bip. var. *sonchoides* (Kunth) Wedd., Chlor. And. 1: 219. 1857. TYPE: Ecuador. Prov. Pichincha: "crescit cum praecedente," 14 Apr. 1802 [Sandwith, 1926], *F. W. H. A. von Humboldt & A. J. G. Bonpland s.n.* (holotype, P!, P photos LP!, MO!).

Achyrophorus barbatus Sch. Bip., Jahresber. Pollichia 16–17: 48. 1859. *Achyrophorus sessiliflorus* (Kunth) DC. var. *barbatus* (Sch. Bip.) A. Gray, Proc. Amer. Acad. Arts 5: 146. 1861. *Hypochaeris barbata* (Sch. Bip.) Reiche, Anales Univ. Chile 116: 589. 1905. TYPE: Colombia. Dept. Norte de Santander: "Nova Granada, prov. Pamplona in Paramo de San Urban," 11,000 ft., Dec. 1842, *J. J. Linden* 746 (lectotype, designated here, P!; isotypes, BM [2]!, K [2]!, P!, W!, W photo MO!).

Hypochaeris stuebelii Hieron., Bot. Jahrb. Syst. 21: 373. 1896. TYPE: Ecuador. Prov. Napo: "crescit in Páramo montis Antisana," Oct. 1871, *M. A. Stübel* 184b (holotype, B [presumably destroyed], B photos LP!, MO!).

Herbs to 13 cm tall. Leaves linear-lanceolate or elliptic-lanceolate, 20–130 × 5–25 mm, attenuate in a broad petiole with conical trichomes, margins dentate to slightly dentate, both surfaces glabrous or with some glandular trichomes. Capitula sessile or pedunculate (to 10 cm); bracts on peduncle linear, with long shaggy trichomes to 6 mm or glabrous; involucre campanulate to hemispheric, 13–25 × 10–25 mm; phyllaries 3- to 4-seriate; outer and middle phyllaries oblong-lanceolate to lanceolate, 7–15 × 2–4 mm, with shaggy trichomes on midribs to near apex or glabrous, at margins ciliate; inner phyllaries linear-lanceolate to linear, 11–25 × 2–4 mm, glabrous or sparsely ciliate at margins, often divided at the apex; paleae 12–23 mm; florets ca. 25. Corollas usually

yellow or white, rarely orange or purple, 12–27 mm; tube 5.5–13 mm; ligule 6.5–14 mm; vascularization type 1; stamens 7–19 mm; anthers 2.5–9 mm; basal appendages types 2 and 3, 0.5–1 mm; filaments 5–14 mm; antheropodium types 1 and 2. Styles 9–22 mm with branches 1–2.5 mm. Cypselae 5-ribbed, semirostrate, rostrate, or erostrate, 2–7 mm; walls scaly or smooth; pappus 7–18 mm. Chromosome numbers $2n = 8, 16$ (Jansen & Stuessy, 1980; Olsen, 1980; Weiss et al., 2003; Weiss-Schneeweiss et al., 2007, 2008).

Habitat and distribution. *Hypochaeris sessiliflora* has been found from Venezuela to Bolivia, in drier places, between 2000 and 4500 m (Fig. 4A).

Phenology. *Hypochaeris sessiliflora* flowers throughout the year.

Common names. "Achicoria" (Ecuador, *Peñafiel et al.* 382); "cachu-cachu" (Peru, *Macbride & Featherstone* 1791); "chicorea" (Colombia, *Soejarto* 494); "chicoria" (Venezuela, *Jahn* 146); "chicoria blanca" (Venezuela, *Aristeguieta* 2438). The white latex is reported as being used for toothache (Ecuador, *Ellemann* 91672).

Morphological characters. *Hypochaeris sessiliflora* is distinguished from other species of the complex by having leaves that are linear-lanceolate (or less often elliptic-lanceolate), glabrous, and toothed or slightly toothed at the margin, and cypselae that are cylindrical.

Hypochaeris sessiliflora is the most polymorphic with respect to vegetative and reproductive characters (especially shape and pubescence of leaves and phyllaries, and variation in floral color) of all members of the *H. sessiliflora* complex (Fig. 3B–D). The heads can be pedunculate (to 10 cm) or sessile, the outer phyllaries can have the margin hyaline or opaque, and in some populations (described as *H. stuebelii* by Hieronymus, 1896) the phyllaries are inflated with the apex either divided or entire. Another variable character is the color of corollas, with white, yellow, or rarely purple often encountered in the same population. *Hypochaeris sessiliflora* var. *barbata* (described as *Achyrophorus barbatus*, *Schultz Bipontinus*, 1859) was characterized by having linear peduncular bracts with long shaggy trichomes to

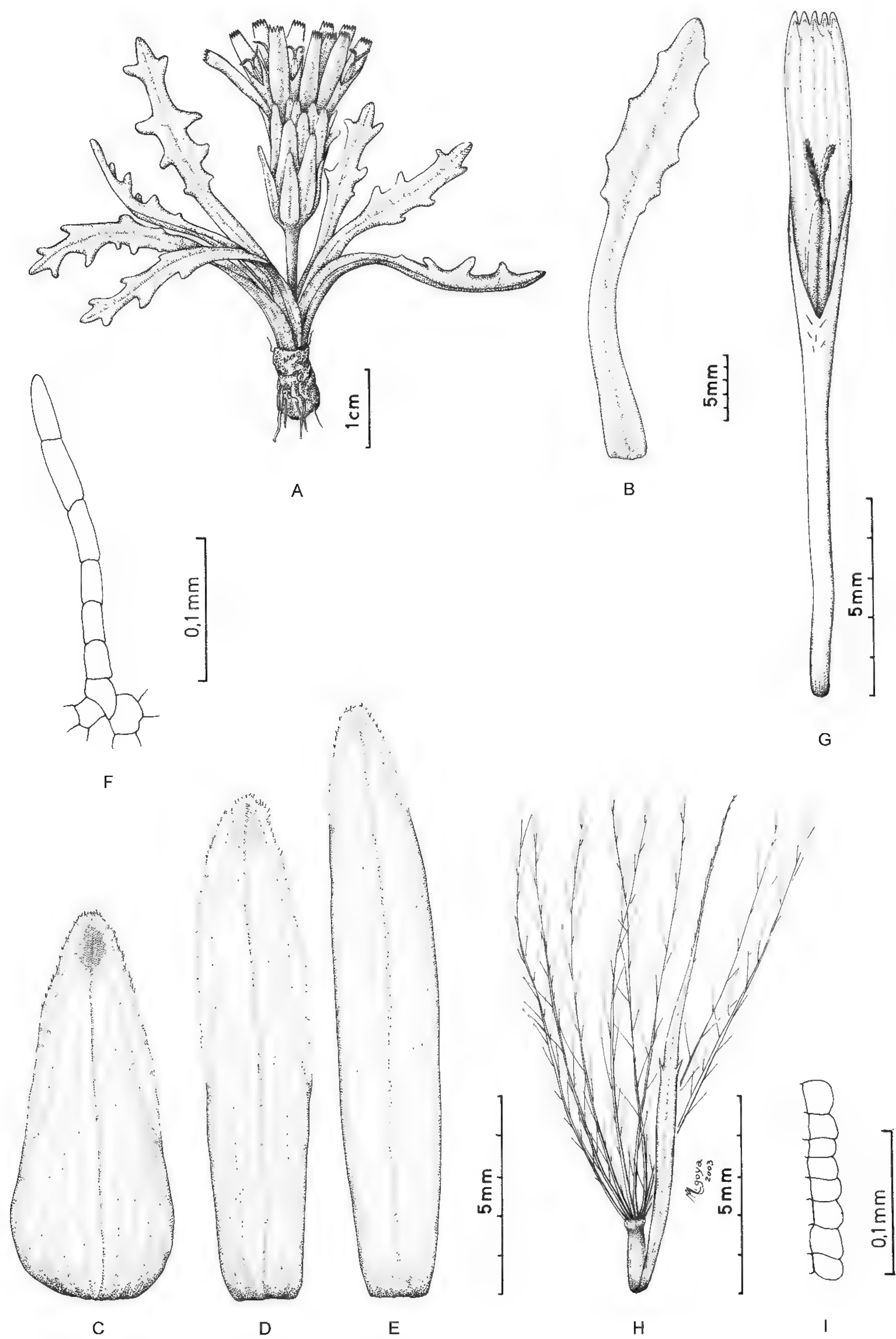


Figure 5. *Hypochaeris taraxacoides*. —A. Habit. —B. Leaf. —C–E. Phyllaries. —F. Trichomes (in cilia) on phyllaries. —G. Corolla with anthers and style. —H. Palea, cypselae, and pappus. —I. Smooth cypselar wall. From *Stuessy et al. 18074* (LP).

6 mm, setaceous phyllaries with yellow-green and purple trichomes, and outer and middle phyllaries that are divided at the apex (Fig. 3D). Despite these conspicuous morphological features, this form likewise seems to have no geographic integrity; we deem it not worthy of formal recognition. We have seen variation in capitula as represented in Figure 3B–D within a single population on Volcán Pichincha (Stuessy et al. 18539) in Ecuador. Schultz Bipontinus (1845: 120) also struggled with the morphological variation within this species (as *A. quitensis*, nom. illeg.). He recognized a set of unnamed “Formae” in the following manner: I, entire plant glabrous; IIa, heads large; IIb, heads half as small; IIIa, plants subacaulescent; IIIb, plants caulescent. This is a variable species. More populational sampling within its broad geographic range using morphometric and/or molecular analyses would be worthwhile.

Observations. *Hypochaeris sessiliflora* and *H. sonchoides* were published by Kunth (1818) in the same volume (even on the same page), and either could be selected for use (McNeill et al., 2006: Art. 11.5). The former is the much more widely used name, however, and therefore it has been retained.

Schultz Bipontinus (1845: 120) published the names *Achyrophorus quitensis* Sch. Bip., *Scorzonera quitensis* Humb., and *S. sessilis* Humb. under *Hypochaeris sessiliflora*. Because they were not accompanied by descriptions or specimens, they remain prosynonyms. *Hypochaeris sessiliflora* f. *caulescens* Hieron. (Bot. Jahrb. Syst. 28: 658. 1901) is another invalid name because it was published without description.

Schulz Bipontinus (1859: 52) also published *Achyrophorus albiflorus* Sch. Bip. and *A. humboldtii* Sch. Bip., but both are nom. illeg., being superfluous names of *A. quitensis* Sch. Bip., which itself is illegitimate, having been cited in synonymy of *Hypochaeris sessiliflora*. Bortiri (1997) lectotypified both *A. albiflorus* and *A. humboldtii*, but being illegitimate, this is unnecessary. *Hypochaeris sessiliflora* var. *albiflora* Hieron. (Bot. Jahrb. Syst. 28: 658. 1901), therefore, is also an illegitimate name.

Reiche (1905) may have had a confused concept of *Hypochaeris barbata*, as he cited it as occurring in northern Chile (Prov. [– Region] Tarapacá), where *H. sessiliflora* is not known to occur (Fig. 4A); he probably had material of *H. eremophila*, as he cited *Distoecha taraxacoides* Phil. in synonymy.

Representative specimens. BOLIVIA. **Cochabamba:** Tunari [probably Cerro Tunari], Müsch 151 (p.p., SI). COLOMBIA. **Boyacá:** entre Gachoque y Toca, Zuloaga & Landon 4136 (SI). **Caldas:** Nevado del Cocuy, alto valle de Las Lagunillas, Cuatrecasas 1484 (US). **Cauca:** Cordillera Central, E slopes of páramo del Purace, around la laguna de

San Rafael, Cuatrecasas & Willard 26299 (US). **Cundinamarca:** Páramo de Chisacá, Soderstrom 1254 (NY). **Magdalena:** Sierra Nevada de Santa Marta, valley descending SW from Pico Reina and Ojeda, Cuatrecasas & Romero Castaneda 24560 (US). **Nariño:** Pasto, volcán de El Galeras above Pasto, Ewan 16324 (US); Pasto, Volcán Galeras, Plowman 1955 (US); University of Nariño property, vic. Granja Botana, 3.5 km down rd. from entrance, ca. 7 km S of Pasto, Leiteyn, Dumont & Buritica 4995 (NY). **Santander:** Páramo de Mogotocoro, near Vetás, Killip & Smith 17641 (US); Molina & Barkley 18 S.388 (US). ECUADOR. **Azuay:** Cuenca, Parroquia Baños, hacienda de Yanasacha, Boecke & Jaramillo 2493 (US). **Azuay-Loja:** Nudo de Cordillera Occidental y Cordillera Oriental entre Oña y Rancho Ovejero, Barclay & Juajibioy 8472 (US). **Carchi:** Julio Anrade-playón de San Francisco rd., La Palestina, Boelke & Jaramillo 2348 (NY). **Chimborazo:** along the rd. to Riobamba, ca. 20 km SW of Riobamba, King & Garvey 6968 (US). **Cotopaxi:** 5.5 km E of Pujilí, Stuessy et al. 18549 (LP, WU). **Imbabura:** Cotacachi Canton, Res. Ecol. Cotacachi-Cayapas, laguna de Cuicocha, Peñafiel et al. 382 (US). **Loja:** 12 km NW of Saraguro on loma Paredones, Ellemann 91672 (US). **Napo:** Tena Cantón, Parque Nac. Llaganates, vía Salcedo-Tena, de laguna Chaloa Cocha desvío a Rayo Filo, Vargas, Narváez & Orellana 2619 (NY, US). **Napo-Pastaza:** alrededores de Los Llanganati, entre Ainchilibí y Río Portrero, E de Romo Páramo, Barclay & Juajibioy 9210 (US). **Pichincha:** 23 km E of Pifo, Stuessy et al. 18540 (WU). **Tungurahua:** Patate Cantón, Parque Nac. Llanganates, laguna de Aucacocha-cerro Pan de Azúcar, Vargas, Ronquillo & Granda 2887 (US). PERU. **Amazonas:** Chachapoyas, Quebrada Molino, 5 km below Chachapoyas, Wurdack 761 (US). **Ancash:** Huaylas, distr. Pamparnas, path Karka to laguna Negra Huacanam, around the laguna itself, Weigend 2000/616 (NY). **Celendín:** 17–24 km from Celendín, Smith & Cabanillas 7328 (US). **Cuzco:** Cuzco, alrededores de las ruinas de Sacsahuamán, Beck 8356 (LPB). **Junín:** Huancayo, Killip & Smith 23369 (US). **Lima:** Río Blanco, Killip & Smith 21680 (US). **Puno:** Cavasaya, hda. Sojela, Vargas 21784 (LP). VENEZUELA. **Apure:** a lo largo del Río Talco (Oirá) y sus afluentes, en páramos entre Alto de Cruces y Tierra Negra, Steyermark & G. C. K. & E. Dunsterville 101105 (NY). **Mérida:** Mérida, páramo at laguna de Mucubaji, near Apartaderos and San Rafael, 35 km NE of Mérida, Maguire 39405 (NY).

2. *Hypochaeris taraxacoides* Ball, J. Linn. Soc., Bot. 22: 48. 1885. *Oreophila taraxacifolia* Meyen & Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(suppl. 1): 291. 1843, non *Oreophila taraxacifolia* Loisel., 1827. TYPE: “Peruvia: in planitie circa Tacoram,” 14,000–17,000 ft., 1831, F. J. F. Meyen s.n. (holotype, B [presumed destroyed, Stafleu & Cowan, 1981]). Figure 5.

Hypochaeris stenocephala (A. Gray ex Wedd.) Kuntze var. *integrifolia* Kuntze, Revis. Gen. Pl. 3(2): 160. 1898. *Hypochaeris stenocephala* (A. Gray ex Wedd.) Kuntze var. *taraxacoides* (Meyen & Walp.) Kuntze, Revis. Gen. Pl. 3(2): 160. 1898. TYPE: Bolivia. Dept. Oruro: Oruro, 1892, C. E. O. Kuntze s.n. (holotype, NY!).

Herbs to 7 cm tall. Leaves lanceolate or oblong, 1.5–11 × 0.3–1.2 cm, pinnatifid to lobate, glabrous, at base attenuate. Capitula pedunculate to 40 mm;

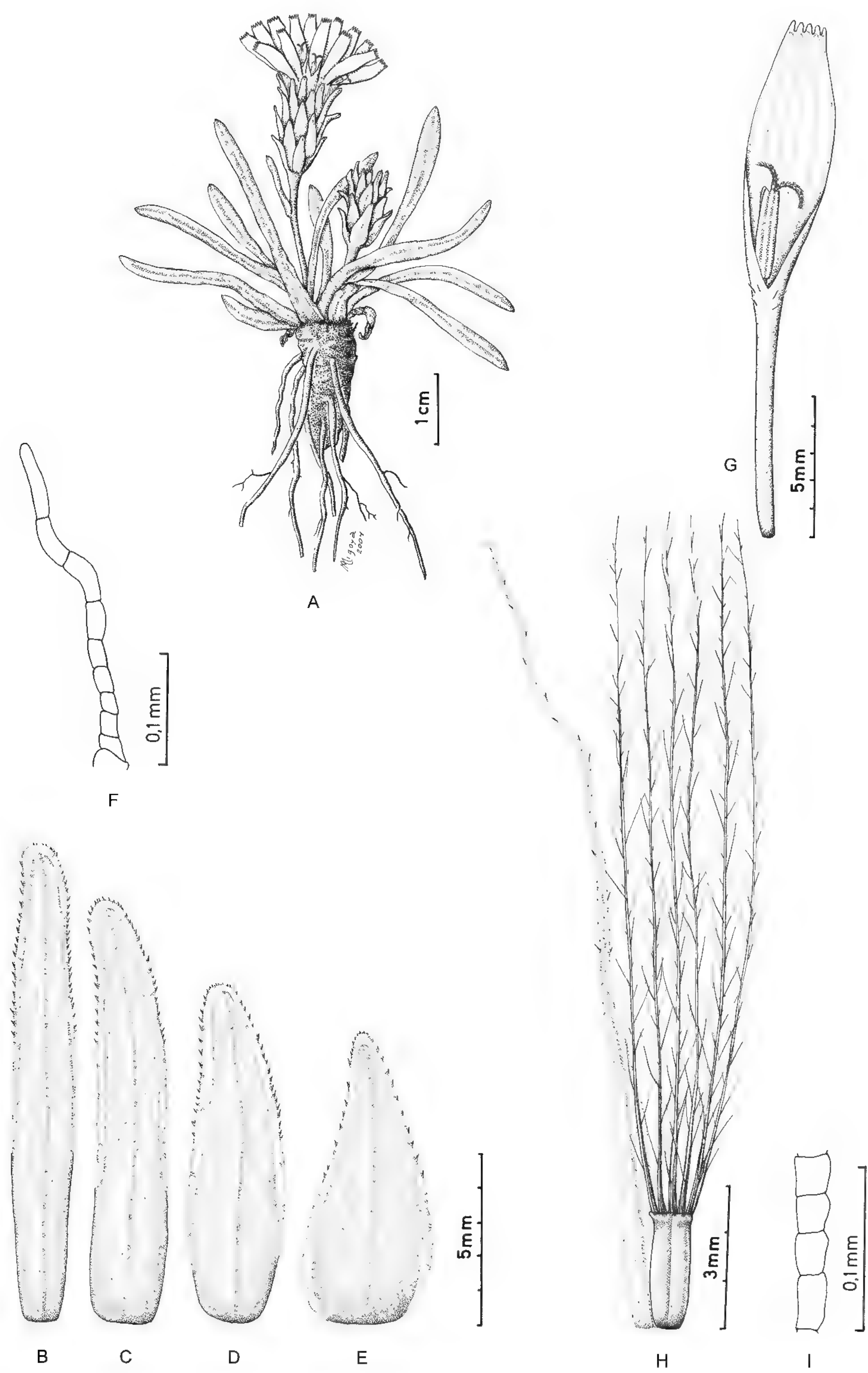


Figure 6. *Hypochaeris hohenackeri*. —A. Habit. —B–E. Phyllaries. —F. Cilia on phyllaries. —G. Corolla with anthers and style. —H. Palea, achene, and pappus. —I. Smooth cypselar wall. From *Lewis 35168* (LP).

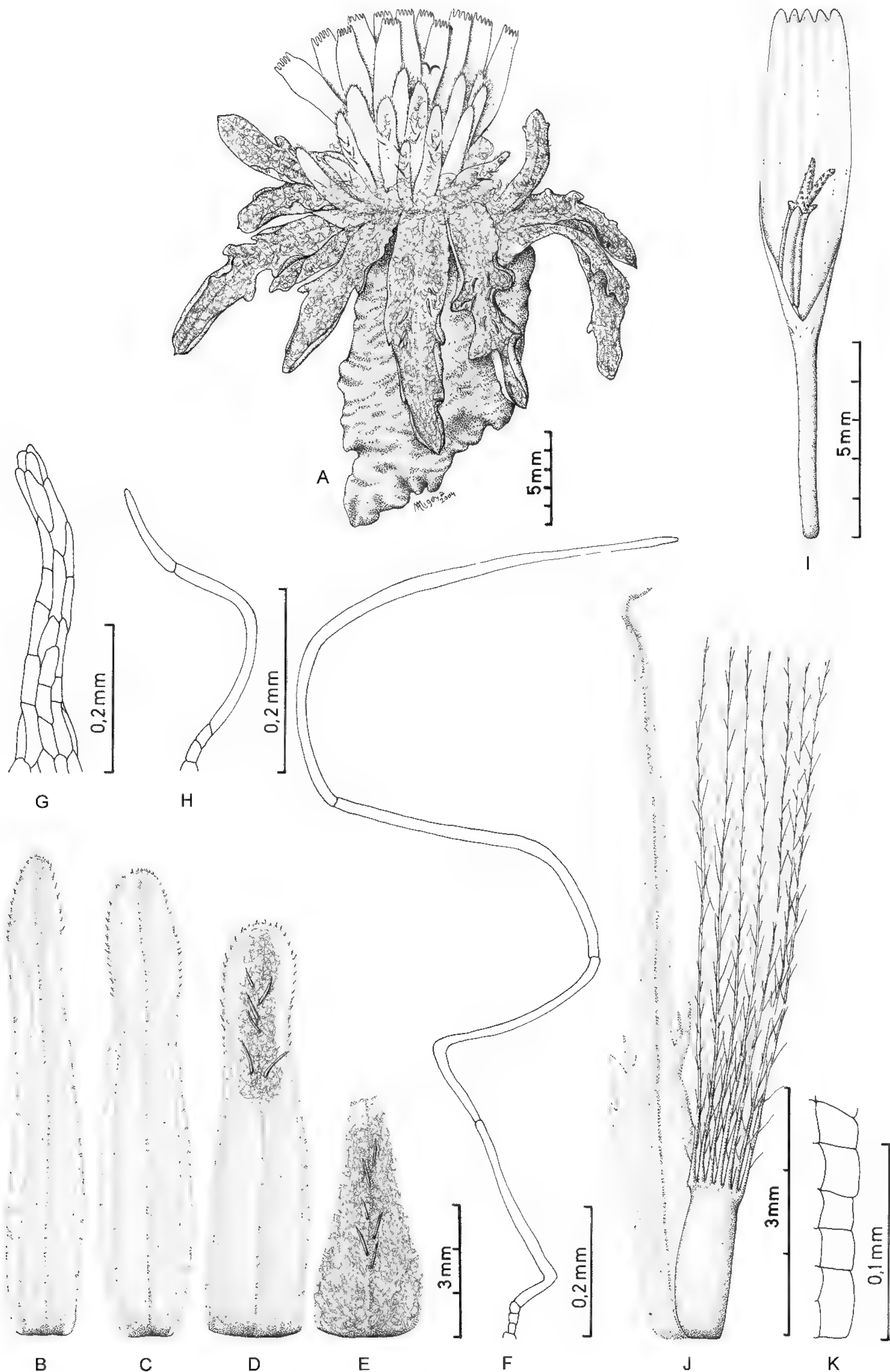


Figure 7. *Hypochaeris mucida*. —A. Habit. —B–E. Phyllaries. —F. Whip trichomes on phyllaries. —G. Shaggy trichomes on phyllaries. —H. Trichomes (in cilia) on phyllaries. —I. Corolla with anthers and style. —J. Palea, cypselae, and pappus. —K. Smooth cypselar wall. From Ceballos et al. 614 (SI).

involucre cylindrical, 14–23 × 5–10 mm; phyllaries 3- to 4-seriate, lanceolate, apex rounded, margin ciliate; outer phyllaries 8–11 × 2–3 mm; inner phyllaries 15–19 × 3–3.5 mm; paleae 12–18 mm; flowers ca. 30 per capitula. Corollas white (upper surface) to dark blue-black at tips of ligules underneath, 15–21 mm; tube 7–9 mm; ligule 8–12 mm; vascularization type 2; stamens 10–17 mm; anthers 4–5 mm; basal appendages type 3, ca. 1 mm; filaments 6–12 mm; antheropodium type 1; style 12–22 mm, with style branches 1.8–2 mm. Cypselae erostrate, 1.8–2 mm; wall smooth; pappus 12–17 mm. Chromosome number $2n = 8, 16$ (Parker, 1971; Weiss et al., 2003 [as *Hypochaeris stenocephala*]; Weiss-Schneeweiss et al., 2007, 2008).

Habitat and distribution. *Hypochaeris taraxacoides* inhabits bogs and seeps from Colombia to northern Chile and northwestern Argentina, 2640–5000 m (Fig. 4B, circle).

Phenology. *Hypochaeris taraxacoides* flowers throughout the year.

Common names. “Achicoria” (Argentina, *Haber 142*); “chicoria” (Peru, *Mexia 4191*); “diente de león” (Bolivia, *Schulte 9*); “flor de ciénaga” (Argentina, *Cabrera et al. 22484*); “lechero” (Argentina, *Haber 5*); “mula-siki” (Bolivia, *Wolstenholme 6*); “pilly” (Peru, *Mexia 4191*).

Morphological characters. *Hypochaeris taraxacoides* is readily distinguishable from other taxa by the combination of peduncular (rarely sessile) cylindrical heads, glabrous phyllaries (ciliate on margins) and leaves, and corollas white on the upper surface to dark blue-black at the tips of ligules underneath (abaxial surface), and being longer than the involucre.

Observations. Although no isotype has been located, the detailed description and locality combine to leave no doubt as to the biologic affinity of this name. The locality of plains near “Tacoram” presumably refers either to the town of Tacora and/or Volcán Tacora, both of which are now within the boundaries of Chile, Region I, Parinacota Province (just across the border from Peru), Tacna Department. At the time of collection and for another half century, this region was within Peru (e.g., Enock, 1908: cf. map). Ratzeburg (1843: xviii) tells us that Meyen went up from Arica, Chile, toward Lake Titicaca, and Tacora is on this route. This species is known from this general region (Fig. 4B, circle).

In publishing *Achyrophorus taraxacoides* Walp. (Repert. Bot. Syst. 6: 336. 1846, nom. illeg.) [non *A. taraxacoides* (D. Don) Steud. (Steudel, 1841: 226)], Walpers (1846) purported to make a new combination based on *Oreophila taraxacoides* Meyen & Walp., but

gave reference to the place of publication of *O. taraxacifolia* Meyen & Walp. Whether or not this incorrect epithet used in the combination should be treated as an error to be corrected to “*A. taraxacifolia*” or considered deliberate in view of the existence of *A. taraxacifolia* Moench (Moench, 1802) is unimportant because, in either case, the name is illegitimate, with Steudel having validly published the name *A. taraxacoides* five years earlier. *Hypochaeris taraxacoides* (Walp.) Benth. & Hook. f. (Gen. Pl. 2: 519. 1873) has also been used in some reports (e.g., Bortiri, 1999, as synonym) and in much herbarium material, but this also uses the incorrect epithet in combination. More importantly, Bentham and Hooker (1873: 519) did not actually make the combination. They only listed “...in *Achyrophoro taraxacoides*, Walp.” under *Hypochaeris* (as “*Hypochoeris*”), a particular technique in this work that is specifically disallowed as a new combination in Article 33.1 of the *International Code of Botanical Nomenclature* (and exemplified in McNeill et al., 2006: Art. 33, Ex. 2). The first publication of a legitimate name for the species in *Hypochaeris* followed shortly thereafter: *H. taraxacoides* Ball (J. Linn. Soc., Bot. 22: 48. 1885). It is curious that Walpers, one of the two original authors, cited the original epithet *taraxacifolia* incorrectly when transferring it into *Achyrophorus*, and in this was followed by Bentham and Hooker and Ball under *Hypochaeris*. They may have been aware of the earlier competing name, *H. taraxacifolia* Moench (Suppl. Meth. 224. 1802), now referable to *Crepis albida* Vill. (Babcock, 1947: 310) or to the earlier *O. taraxacoides* D. Don, which does not belong to the *H. sessiliflora* complex, but there is no evidence of this. It is fortunate for maintaining stability of usage that *H. taraxacoides* Ball can be treated as a new name in 1885, for a new combination based on the epithet that was actually used would have resulted in the illegitimate *H. taraxacifolia* (Meyen & Walp.) Ball, a later homonym of *H. taraxacifolia* Moench (Moench, 1802). An earlier *H. taraxacoides* Pourr. ex Steud. (Nomencl. Bot. [Steudel], ed. 1, 422, 618. 1821) also exists, but appears as a synonym of *Picridium albidum* DC. (– *Crepis albida* Vill., Babcock, 1947: 310); the name is not validly published and so creates no competing difficulty.

Achyrophorus stenocephalus A. Gray ex Wedd. is an invalid name because it was listed by Weddell (1857) as synonym under *Achyrophorus taraxacoides* (Meyen & Walp.) Walp. *Hypochaeris stenocephala* (A. Gray ex Wedd.) Kuntze [Kuntze, 1898]), therefore, is an illegitimate combination.

The characters used by Kuntze (1898: 160) to differentiate *Hypochaeris stenocephala* var. *integrifolia* from variety *taraxacoides* are leaf margins entire or

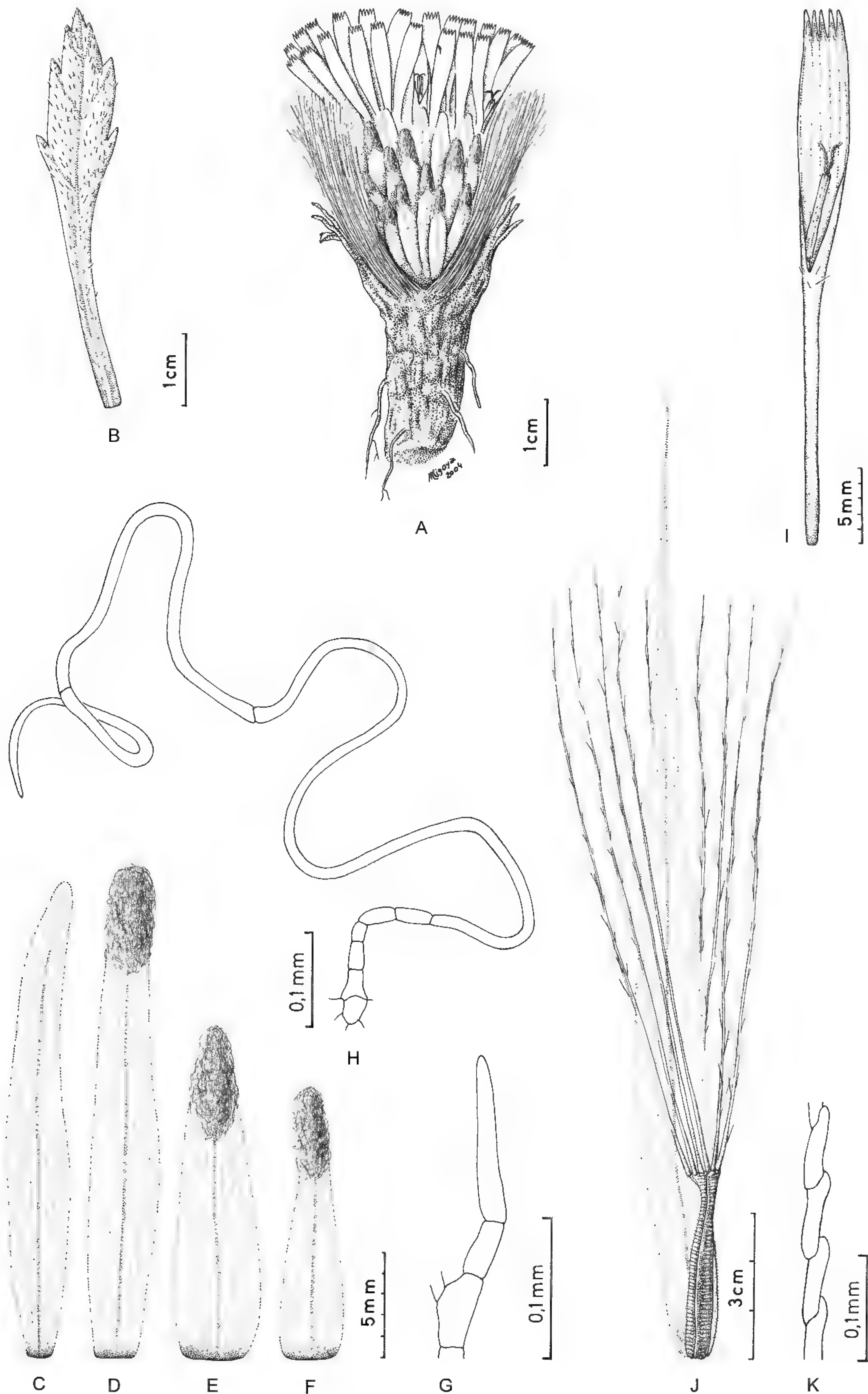


Figure 8. *Hypochaeris eriolaena*. —A. Habit. —B. Leaf. —C–F. Phyllaries. —G. Trichomes (in cilia) on phyllaries. —H. Whip trichomes on phyllaries. —I. Corolla with anthers and style. —J. Palea, cypselae, and pappus. —K. Smooth cypselar wall. From Smith & Buddensiek 11133 (LPB).

denticulate versus runcinate, respectively, which were essentially validating the listed, but not named, varieties in *Achyrophorus taraxacoides* (Meyen & Walp.) Walp. by Weddell (1857). This variable feature (leaf margin) is insufficient for varietal recognition.

The name *Hypochaeris taraxacoides* (Meyen & Walp.) Ball var. *lanuginosa* Herzog is a nomen nudum because it was only mentioned in a list of Bolivian plants published by Herzog (1923: 228).

Representative specimens. ARGENTINA. **Catamarca:** Antofagasta de la Sierra Hoyada de Antofagasta, *Haber* 5 (SI). **Jujuy:** Capital, refugio del nevado de Chañi, *Fabris, Cano & Tello* 4035 (LP); Cochinoca, Abra Pampa, cerro Huancar, *Cabrera et al.* 15256 (LP); Humahuaca, 31.4 km W of Humahuaca on gravel rd. to El Aguilar, *Stuessy, Urtubey & Tremetsberger* 18089 (LP, WU); Humahuaca, 0.8 km NW of Chiapi Rodeo on dirt rd. to Iruya, *Stuessy, Urtubey & Tremetsberger* 18074 (LP, WU); 4.7 km NW of Chiapi Rodeo on dirt rd. to Iruya, *Stuessy, Urtubey & Tremetsberger* 18075 (LP, WU); Iturbe, *Meyer, Cuezio & Legname* 21040 (LP); Rinconada, Mina Pirquitas, *Schwabe, Ancibor & Vizinis* 641, 818, 819 (LP); Tilcara, lecho de Río Grande cerca de Huacalera, *Werner* 820 (LP); Tumbaya, camino de El Angosto al Chañi, encrucijada Río Chañi, *Cabrera et al.* 22484 (LP); Valle Grande, Caspalá, *Burkart & Troncoso* 11822 (SI); Yavi, Quebrada de Toquero, A. L. & S. M. *Cabrera, Malacalza & von Schmiden* 17656 (LP); Lecho, 1–2 km S RP 5, Km 13, 4–5 km SW de Yavi, *Tolaba, Acuña, Arapa, Gutiérrez, Quiroga, Ragno, Ramallo & Da Silva* 1539 (MCNS). **La Rioja:** Famatina, Sierra de Famatina, *Rohweder T-12* (LP). **Salta:** Los Andes, Vega de Tocomar, *Cabrera et al.* 22531 (LP); Poma, Quebrada entre Muñaño y Tastil, *Cabrera* 8993 (LP); San Antonio de Los Cobres, San Antonio de Los Cobres, *Krapovickas* 3155 (K, SI); Santa Victoria, 43.7 km from Santa Victoria on rd. to La Quiaca, *Hawkes, Hjerting & Rahn* 3900 (K, LP). **Tucumán:** Tafí, Cerro Muñoz, La Banda, *Fabris* 1520 (LP). BOLIVIA. **Cochabamba:** Chapare, Quebrada de Colomi, *Balls B-6253* (K, UC); Quillacollo, 63 km de Cochabamba en dirección al poblado de Cami, alrededores del cerro Pytuljata, *Liberman* 2343 (LPB, US); Tapacarí, Qachi uñkata, cerca del Río Chankha, 3 km al E de Japo K'asa, *Pestalozzi* 284 (LPB). **La Paz:** Aroma, Kanton Callamarca, 6 km nördlich Calamarca an der Straße La Paz-Oruro, *Krach* 7492 (SI); Camacho, Puerto Acosta, 10 km hacia La Paz, al borde del Río Huaycho, cerca del Lago Titicaca, *Beck* 7712 (SI); Fray Tamay, Pelechuco, *Krach* 9391 (SI); Ingavi, low ridge along the main rd. from La Paz to Viacha, ca. 8 km NE of Viacha, *Solomon & Nee* 14233 (LPB, NY); La Paz, Palca, zona basal del Illimani, *Ceballos et al.* 548 (SI); Pacajes, La Paz entre Corocoro y Topohoco, *Ceballos et al.* 164 (SI); Los Andes, Kanton Peñas, Straße zur Mina Fabulosa, Km 6.5 von der Abzweigung von der Straße La Paz-Huarina, *Krach* 8435 (SI); Larecaja, viciniis Sorata, inter Ancohuma et Turilaque, *Mandon* 276 (BM, K, W); Murillo, 4.6 km S jct. rd. to Chacaltaya on rd. from Milluni to El Alto (La Paz), *Solomon* 13177 (LPB); Nor Yungas, Canton Pocollo, La Cumbre, *Krach* 8672 (SI); Omasuyos, Cantón Huarina, comunidad de Moco-Moco, *Loza de la Cruz* 72 (LPB); Tamayo, Ulla-Ulla, estribaciones de la cordillera de Apolobamba, *Menhofer* 1036 (LPB); Saavedra, bei Curva großes Moor oberhalb der Endnoränen oberhalb Canizaya, *Freueller* 4384 (SI); Tamayo, Ulla-Ulla, Okaria, *Menhofer* 1600 (LPB). **Oruro:** Sajama, Cantón Lagunas, puna y

vegetación alto andina, *Loza de la Cruz* 254 (LPB). **Potosí:** Frías, cerro Khare-Khare detrás de la ciudad, *Schulte* 9 (LPB). **Tarija:** José María Avilez, Pampa Tajzara, Arenales, *Beck & Paniagua* 27086 (LPB). COLOMBIA. **Boyacá:** Cordillera Oriental Páramo de Huma, entre Belén y Susacón, *Barclay & Juajibioy* 7642 (US). PERU. **Ancash:** along Perú hwy. 105 to Chavin de Huantas, ca. 26 km E of Catac, *King & Collins* 9064 (US). **Arequipa:** Arequipa, just SW of Puno border, Paso del Cóndor, *Iltis & Ugent* 1489 (UC). **Ayacucho:** ca. 10 km N of Mataral, on trail to Ayacucho, *West* 3663 (UC). **Cuzco:** Urubamba, *Zamalloa Díaz* 78 (LP); Chanchis, La Raya pass 1 km WNW of La Raya on Cuzco rd., *Iltis & Ugent* 1256 (US); Chumbivilcas, 15 km de Sto. Tomás a Yairi, *Hoogte & Roessch* 2534 (NY); Paucartambo, Paucartambo, Accanaco, *Balls B6711* (K). **Huancavelica:** Huancavelica, Ojapampa, entre Laria y Tambopata, a 25 km de Conaica, *Tovar* 850 (LP [2]); Tayacaja, quebradas westward from Huancavelica, *Stork & Horton* 10838 (UC). **Huancayo:** Huancayo, 30 km N of Huancayo, *Blair* 636 (K). **Huánuco:** Huánuco, 15 mi. NE of Huánuco, *Macbride & Featherstone* 2167 (US). **Junín:** Concepción, Km 112, rd. Concepción–Satipo, *Saunders* 1106 (K, UC); Junín, Capillacocha, a 20 km E of Carhuamayo, *Tovar* 390, 393 (LP); Llanos de Junín, 76°00'W, 11°10'S, *Smith et al.* 5652 (NY); Tarma, lago Junín, 13 km N of Junín, *Hutchison, Wright & Straw* 5892 (UC); Yauli, Jaranacu, cerca de Chacalpa, *Ochoa* 264 (US). **La Libertad:** Bolivar, laguna de Loa Ichus Nevado, Cajamarguilla, *López & Sagástegui* 3223 (LP); Pataz, Huancaspata–Tajabamba, *López & Sagástegui* 8245 (LP); Santiago de Chuco, Quesquenda, Jalca Quiruvilca, *López & Sagástegui* 2888 (LP). **Lima:** Canta, Carhuapampa (camino a Canta–Lachaqui), *Mezar* 162 (LP); Yauyos, Huancracha arriba de Tupe, *Cerrate & Tovar* 1174 (LP). **Puno:** Patanca, *Fiebrig* 3188 (BM, K).

3. *Hypochaeris hohenackeri* (Sch. Bip.) Domke, Notizbl. Bot. Gart. Berlin-Dahlem 13: 251. 1936. Basionym: *Achyrophorus hohenackeri* Sch. Bip., Bonplandia 4: 54. 1856. TYPE: Peru. “Tobina in Cordill. sum. jug. [summit ridge],” July 1854, *W. Lechler* 2111a (holotype, P!). Figure 6.

Hypochaeris parvifolia J. Kost., Blumea 5(3): 661, fig. 3c. 1945. TYPE: Bolivia. Dept. La Paz: “Rosettenpolster auf Alpenwiesen im Tcacota-Thal” [most probably Teacota River valley, 16°43'S, 67°25'W, Division of Geography, 1955; protologue gives “Tcacota-Thal,” but label “Teacota-Thal”], 4300 m, Oct. 1911, *T. Herzog* 2425c (holotype, L, digital image!).

Herbs to 4 cm tall. Leaves oblong, 20–30 × 2–3 mm, base attenuate, margin entire or slightly dentate, glabrous. Capitula pedunculate to 20 mm (rarely sessile). Involucre campanulate, 11–15 × 6–8 mm; phyllaries 4- to 6-seriate, lanceolate, apex acute or slightly rounded, margin ciliate; outer phyllaries 8–9 × 2.5–3 mm; inner phyllaries 13–15 × ca. 2 mm; paleae 11–15 mm; florets ca. 15 per capitula. Corollas yellow, rarely pink (*Smith & Cabanillas* 7212), 10–20 × 3–8 mm; ligule 7–12 mm; vascularization type 1; stamens 11.5–20.5 mm; anthers 8–12 mm; basal appendages type 1 or 2, 0.50–0.75 mm; filaments 3.5–8.5 mm; antheropodium type 1 or 2; style 10–12 mm; style branches

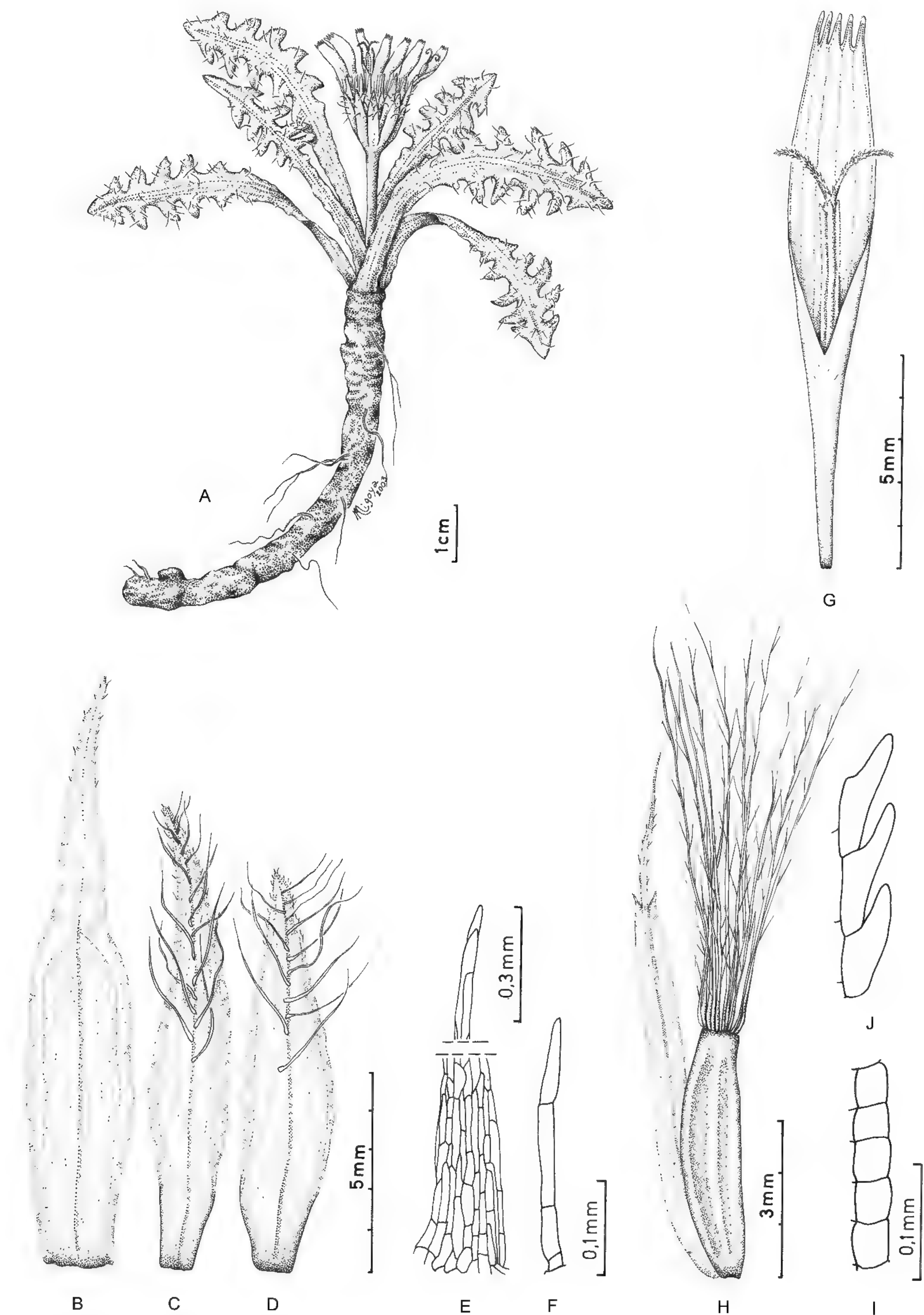


Figure 9. *Hypochaeris echegarayi*. —A. Habit. —B–D. Phyllaries. —E. Shaggy trichomes on phyllaries. —F. Trichomes (in cilia) on phyllaries. —G. Corolla with anthers and style. —H. Palea, achene, and pappus. —I. Smooth cypsellar wall. —J. Scaly cypsellar wall. A–H, J from Valenzuela 998 (LPB); I from Hunziker & Caso 6039 (LP).

1.5–2.5 mm. Cypselae erostrate, 2–2.5 mm; wall smooth; pappus 9.5–15 mm. Chromosome number unknown.

Habitat and distribution. *Hypochaeris hohenackeri* occurs from Peru to Bolivia, 3200–4500 m, in humid grasslands, mountain pastures, riverbanks, and bogs associated with *Juncus* L. and *Stipa* L. (Fig. 4B, squares).

Phenology. *Hypochaeris hohenackeri* flowers from January to September.

Morphological characters. *Hypochaeris hohenackeri* is characterized by oblong, sometimes dentate, leaves, a pedunculate head (rarely sessile), and dark, glabrous phyllaries that are acute or rounded at the apex.

Observations. *Achyrophorus hohenackeri* ["*Hohe-nackeri*"] was published earlier by Schultz Bipontinus (1855: 236) as a nomen nudum. Although without description, he did cite a specimen (*W. Lechler 2111a*), which was later taken by him (1856: 54) as the original specimen to accompany his valid description (1856: 54) in the same journal. *Hypochaeris hohenackeri* Herzog (Herzog, 1923) is an illegitimate name because no basionym was provided.

Although the type specimen of *Hypochaeris parviflora* J. Kost. is small, there is no doubt of the affinity of this name; the original description is also accompanied by a clear illustration that shows the diagnostic characters of this species.

Representative specimens. BOLIVIA. **Cochabamba:** Arani, near the summit of the pass through the cordillera de Cochabamba, *Eyerdam 24839* (UC). **La Paz:** Inquisivi, along the trail betw. Pongo Chico and laguna Naranjani, ca. 3 km W of Quime, *Lewis 35168* (LPB, NY); W slope of cerro Kharrata SSE, Camillaya, *Müller & Heinrichs 6428* (LPB); 1 km NE of Mina Argentina and 10 km S of Coquetanga, *Lewis 38124* (LPB); Saavedra, el camino de Charazani a Hayrapata, *Menhofer X-1832* (LPB, SI). PERU. **Amazonas:** Chachapoyas, Chachapoyas–Celendín rd., cerro Calla-Calla, *Smith & Cabanillas 7212* (US); cerro de Calla-Calla, betw. Leimebamba–Balsas rd. pass and the camino de herradura, *Wurdack 1225* (LP). **Huancavelica:** Huancavelica, 4 km from Conayca, *Tovar 222* (LP).

4. *Hypochaeris mucida* Domke, Notizbl. Bot. Gart. Berlin-Dahlem 13: 250. 1936. TYPE: Bolivia. La Paz: "Mittlere Anden: Südlich des Titicaca-Sees über Ancoraime," 13,500 ft., 12 Feb. 1903, *A. W. Hill 299* (lectotype, designated here, K!). Figure 7.

Hypochaeris mucida Domke var. *integrifolia* Cuatrec., Proc. Biol. Soc. Wash. 77: 156. 1964. TYPE: Peru. Puno: WSW of Checayani, NE of Azangaro, puno, 4150 m, 29 Mar. 1957, *H. Ellenberg 495* (holotype, U not seen; isotype, US not seen, US photo LP!).

Herbs 1–1.5 cm tall. Leaves oblong, 8–20 × 1.5–4 mm, slightly toothed or pinnatifid, adaxial sur-

face sericeous with whip and some shaggy trichomes, abaxial surface with whip trichomes, petiole sericeous. Capitula sessile. Involucre campanulate, 8–12 × 9–10 mm; phyllaries 3- to 4-seriate; outer phyllaries lanceolate, to 12 mm, lanuginous with shaggy trichomes; inner phyllaries with the same indument or glabrous, margin ciliate. Paleae 9–11 mm; florets ca. 12. Corolla 9.5–11.5 mm, color unknown; tube 3.5–5 mm; ligule 6–6.5 mm; vascularization type 1; stamens 9–10.2 mm, anthers 4–4.2 mm; basal appendages type 1, 0.8–1 mm; filaments 4.5–6 mm; antheropodium type 1; style 8–10.5 mm, with branches 2–3 mm. Cypselae 5-ribbed, unbeaked, 2–3 mm; wall smooth; pappus ca. 8 mm. Chromosome number unknown.

Habitat and distribution. *Hypochaeris mucida* is known from Peru (Puno) and Bolivia (La Paz). It inhabits the Andean steppe at 4150–4700 m, associated with *Pycnophyllum* (Caryophyllaceae) (Fig. 4B, triangles).

Phenology. *Hypochaeris mucida* flowers from February to April.

Morphological characters. *Hypochaeris mucida* is the smallest species of *Hypochaeris*, growing to only 1.5 cm tall. The adaxial surfaces of the leaves and phyllaries are tomentose (with whip and some shaggy trichomes), giving it a distinctive appearance.

Observations. Cuatrecasas (1964) considered *Hypochaeris mucida* var. *integrifolia* to be unique in having leaves entire to sinuate, but this admittedly extreme leaf shape is sporadic and shows no geographic coherence. *Hypochaeris mucida* var. *integrifolia* is not recognized.

The holotype deposited at the Berlin herbarium was destroyed during World War II; the isotype specimen at K is here designated as the lectotype.

Specimens examined. BOLIVIA. **La Paz:** Camacho, Carabuco, Mina Matilde, *Ceballos et al. 614* (SI); Tamayo, Ulla-Ulla, estribaciones de la cordillera de Apolobamba, *Menhofer X-2197* (LPB). PERU. **Puno:** ENE of Checayani, *Ellenberg 638* (US, photo LP).

5. *Hypochaeris eriolaena* (Sch. Bip.) Reiche, Anales Univ. Chile 116: 589. 1905. Basionym: *Achyrophorus eriolaenus* Sch. Bip., Bonplandia 4: 54. 1856. TYPE: Peru. Puno: "Cordiller. pascuis sterilibus pr. Azangaro," June 1854, *W. Lechler 1754* (lectotype, designated by Bortiri [1997: 228], P!; isotypes, K!, P!). Figure 8.

Achyrophorus cryptocephalus Sch. Bip., Bonplandia 4: 54. 1856. *Hypochaeris cryptocephala* (Sch. Bip.) Domke, Notizbl. Bot. Gart. Berlin-Dahlem 13: 251. 1936, as "*cryptocephalus*." TYPE: Peru. Puno: "provincia Carabaya in cacumine Cordill. Agapata [Ayapata]," June

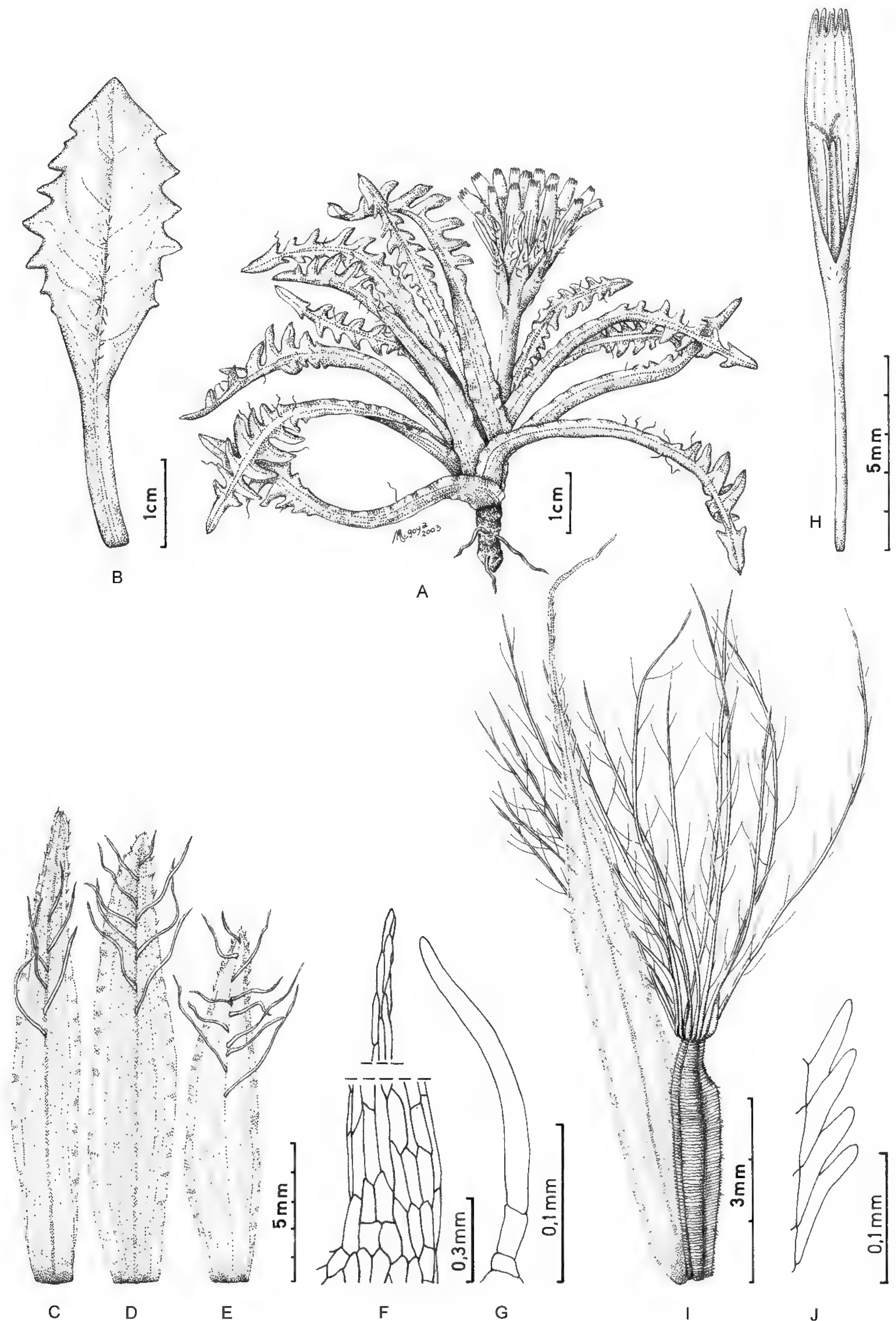


Figure 10. *Hypochaeris eremophila*. —A. Habit. —B. Leaf. —C–E. Phyllaries. —F. Shaggy trichomes on phyllaries. —G. Trichomes (in cilia) on phyllaries. —H. Corolla with anthers and style. —I. Palea, cypselae, and pappus. —J. Scaly cypselar wall. A, C–J from *Stuessy et al.* 18064 (LP); B from *Fabris* 1369 (LP).

1854, W. Lechler 1963 (lectotype, designated here, P!; isotypes, P!, W!).

Hypochaeris spinneri Beauverd, Bull. Soc. Bot. Genève, ser. 2, 14: 177. f. XIII. 1922 [1923]. TYPE: Peru. Huancavelica: Huancavelica, above Huancavelica "in pascuis petrosis," 4700 m, 1915, E. Godet 38 (holotype, presumably NEU, not located).

Herbs to 5 cm tall. Leaves lanceolate or oblongate, 25–70 × 5–16 mm, base attenuate in a broad petiole, margin toothed or entire, glabrous to sericeous (whip trichomes, to 35 mm) or with shaggy trichomes. Capitula sessile. Involucre campanulate or hemispheric, 10–30 × 15–25 mm; phyllaries 4- to 5-seriate; outer phyllaries ovate or lanceolate, lanuginous (with whip trichomes), 5–12 × 2–3 mm; inner phyllaries lanceolate to linear, 12–21 × 1.5–2.5 mm, lanuginous to glabrous, ciliate; paleae 15–28 mm; florets numerous. Corollas white or yellow to golden-yellow, 18–38 mm; tube 8–18 mm; ligule 10–20 mm; vascularization type 2; stamens 11–22 mm; anthers 3–7 mm; basal appendages type 1 or 2, 0.7–1 mm; filaments 8–15 mm; antheropodium type 1 or 2; style 15–26 mm, with branches 1.5–3 mm. Cypselae 5-ribbed, transversely wrinkled, erostrate or slightly narrower at the apex, 1.5–4 mm; wall scaly; pappus 11–29 mm. Chromosome number unknown.

Habitat and distribution. *Hypochaeris eriolaena* occurs in Peru and Bolivia in dry, stony Andean ridges, with scattered grass and limestone outcrops, 2200–5100 m (Fig. 4C, squares).

Phenology. *Hypochaeris eriolaena* flowers from May to November.

Common names. "Cebollana" (Peru, Angulo & López 1358); "qachi tika" (Bolivia, Pestalozzi 606).

Morphological characters. *Hypochaeris eriolaena* is clearly distinguishable from other members of the *H. sessiliflora* complex by long sericeous trichomes on broad petioles plus lanuginous phyllaries. This species often has no developed leaves when the capitulum opens.

Observations. Schultz Bipontius (1859) in his revision of *Hypochaeris* (as *Achyrophorus*) distinguished *H. cryptocephala* from *H. eriolaena* by abaxially sericeous phyllaries in the former and niveous-tomentose phyllaries in the latter. Indument on phyllaries is a variable character in *H. eriolaena*, which can have phyllaries with both lanuginous (with long whip trichomes) and matted indument; furthermore, sometimes phyllaries in the inner series are glabrous. Because of this range of variation, we treat *H. cryptocephala* as conspecific with *H. eriolaena*.

Despite no type having been located of *Hypochaeris spinneri*, the figure associated with the protologue

leaves little doubt of the biological placement of this name.

Hypochaeris eriolaena var. *hispida* Herzog (Herzog, 1923) is a nomen nudum appearing only in a list of plants from Bolivia.

Representative specimens. BOLIVIA. **Cochabamba:** Arque, cerca camino a Tacopaya, *Ibisch & Rojas* 439 (LPB); Tapacarí, Jacha Rancho, comunidad Japo (Km 125 de la carretera Cbba.–Oruro), *Pestalozzi* 606 (LPB). **La Paz:** Achachicala (cumbre), subiendo 3 km de la mina Kaluyo hacia la cumbre, *Beck* 11914 (LPB, SI). CHILE. **Tarapacá:** Cosapilla, Limani, *Wevi* 129 (LP). PERU. **Ancash:** Huaráz-Marcará, *Velarde Núñez* 3225 (LP); Yungay, Yungay-Llanganuco, *López, Sagástegui & Aldave* 7421 (LP). **Cajamarca:** Cajamarca, Majada Pampa, Jalca Alta, *Becker & Terrones* 1433 (US). **Contumazá:** Shanón (arriba de Contumazá), *Sagástegui, Alvitez & Mostacero* 9006 (SI). **Cuzco:** Canchis, en dirección al cementerio (parte alta), *Vargas* 11355 (US); Espinar, alrededores de Yauri, *Vargas* 11350 (p.p.) (US). **Huancavelica:** Huancavelica, Huaytanayoc-Tansiri, Conayca, *Tovar* 2512 (LP). **Junín:** Pampa de Junín, cerro de Pasco and Junín, *Canne & Schunke* 232 (US). **La Libertad:** Otuzco, carretera a Shoreyo, ladera rocosa, *Angulo & López* 1358 (LP); Sánchez Carrión, summit above Aricapampa on rd. to Huamachuco, *Hutchison, Wright & Straw* 6267 (K, US); Santiago de Chuco, Huillillas, N of Cachicadan, *Stork & Horton* 10000 (UC). **Lima:** Canta, La Viuda (cerca de Cullhuay), *Meza* 207 (LP). **Puno:** Puno, San Antonio de Esquilante, *Stafford* 865 (K); Juliaca, Hillside Capachica, Península Lake Titicaca, *Tutin* 1209, 1210 (BM).

6. *Hypochaeris meyeniana* (Walp.) Benth. & Hook. f. ex Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 199. 1874. Basionym: *Oreophila meyeniana* Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(suppl. 1): 292. 1843. *Achyrophorus meyenianus* (Walp.) Walp., Repert. Bot. Syst. 6: 336. 1846. TYPE: "Peruvia: in planitie circa Tacoram," 14,000–17,000 ft., 1831 [one label on type, "4/31," presumably indicating Apr. 1831, but another label in another hand gives "1833"], *F. J. F. Meyen* 22 (holotype, B [presumably destroyed], B photos LP!, MO!). Figure 11.

Achyrophorus meyenianus (Walp.) Walp. var. *ciliatus* Wedd., Chlor. And. 1: 220. 1857. *Hypochaeris meyeniana* (Walp.) Benth. & Hook. f. ex Griseb. var. *ciliata* (Wedd.) Perkins, Bot. Jahrb. Syst. 49: 232. 1913. TYPE: Bolivia. Tarija: "en monte Calama," June 1846, *H. A. Weddell* 4017 (lectotype, designated by Bortiri [1997: 227], P!; isotype, P!).

Hypochaeris meyeniana (Walp.) Benth. & Hook. f. ex Griseb. var. *eriolaenoides* Cabrera, Revista Invest. Agric. 11: 410. 1957. TYPE: Argentina. Jujuy: Sierra de Zenta, 4500 m, Feb. 1931, *E. Budin* s.n. (holotype, LP!; isotype, LP!).

Hypochaeris meyeniana (Walp.) Benth. & Hook. f. ex Griseb. var. *brachylepis* Cabrera, Fl. Prov. Jujuy 10: 677. 1978. TYPE: Argentina. Jujuy: Yavi, "alrededores de La Quiaca," *T. Meyer, A. R. Cuezco & V. Legname* 21270 (holotype, LP!; isotype, LP!).

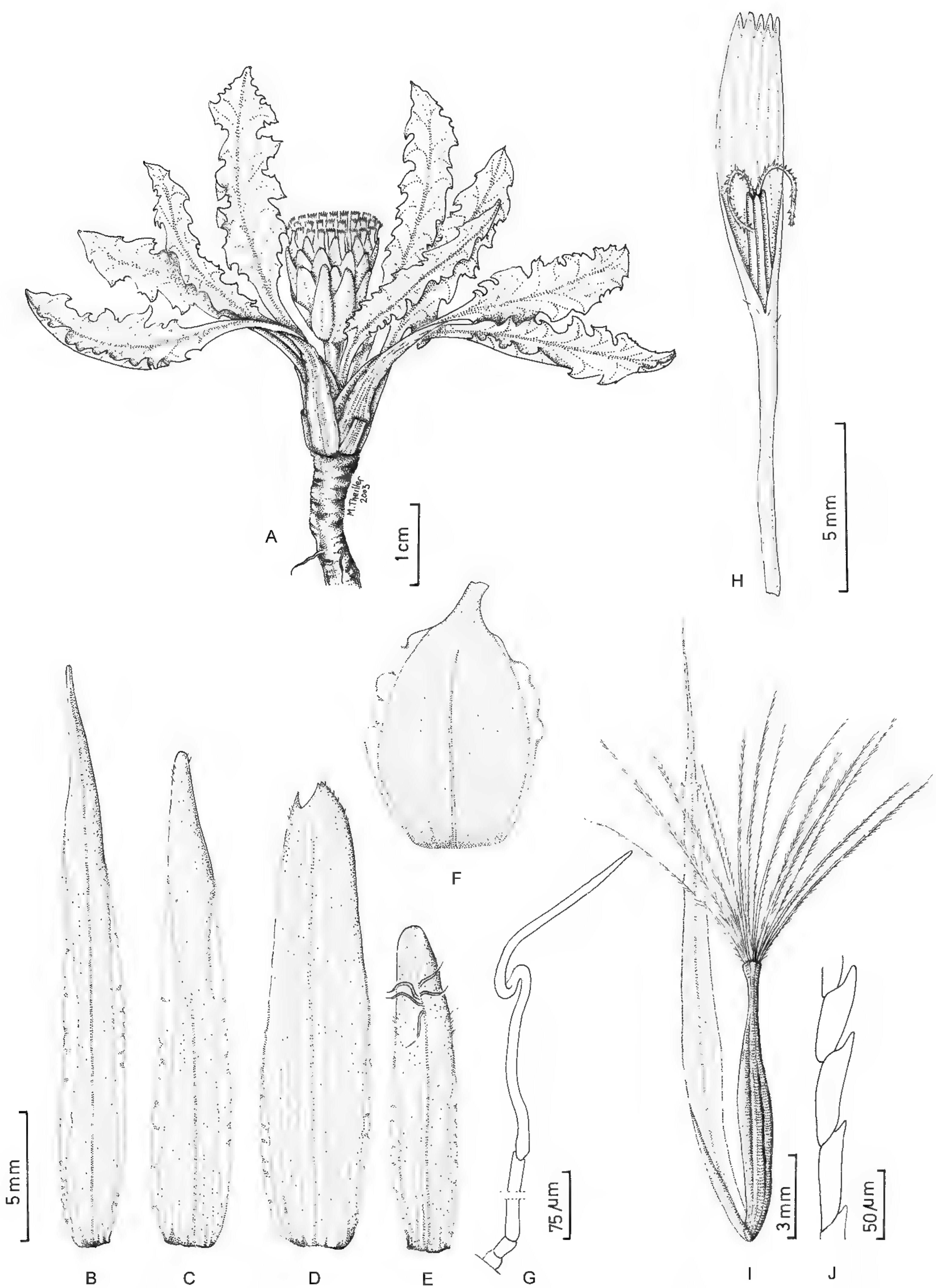


Figure 11. *Hypochaeris meyeniana*. —A. Habit. —B–F. Phyllaries. —G. Trichomes (in cilia) on phyllaries. —H. Corolla with anthers and style. —I. Palea, cypselae, and pappus. —J. Scaly cypselar wall. A–D, G–J from *Stuessy et al. 18062* (LP); E from *Meyer et al. 21306* (LP); F from *Meyer et al. 21107* (LP).

Herbs to 8 cm tall. Leaves lanceolate-elliptic or obovate, 15–150 × 5–40 mm, pinnatisect (rarely pinnatifid), runcinate, base attenuate, margin toothed or entire, glabrous or hispid on the margin (or also on the midrib). Capitula sessile or rarely with a very short peduncule. Involucre campanulate to hemispheric, 8–30 × 8–25 mm; phyllaries 3- to 4-seriate; outer phyllaries lanceolate to ovate, 7–11 × 3–7 mm, attenuate to rounded or acute, glabrous, hirsute (with shaggy trichomes) or lanuginous (with whip trichomes), margin ciliate; middle phyllaries lanceolate to ovate-lanceolate; inner phyllaries lanceolate, 13–22 × 2–2.5 mm, glabrous, slightly ciliate; paleae 13–22 mm; florets ca. 25. Corollas yellow, yellow-orange, or golden-yellow, 13–24 mm; tube 7–11 mm; ligule 6–13 mm; vascularization types 1 and 2; stamens 10–22 mm; anthers 4–6 mm; basal appendages types 2 and 3, 0.3–1 mm; filaments 6–16 mm; antheropodium type 1; style 11–22.5 mm, with branches 2–4.5 mm. Cypselae slightly constricted at apex, 2–10 mm; wall scaly or smooth; pappus 7–17 mm. Chromosome numbers $2n = 8, 16$ (Diers, 1961; Weiss et al., 2003; Weiss-Schneeweiss et al., 2007).

Habitat and distribution. *Hypochaeris meyeniana* occurs from Peru to northwestern Argentina, on rocky and/or sandy slopes, in dry and humid places, 1700–4800 m (Fig. 4D). *Hypochaeris meyeniana* grows sympatrically with *H. taraxacoides*, but they occupy different microhabitats, dry places versus bogs, respectively.

Phenology. *Hypochaeris meyeniana* flowers throughout the year.

Common names. “Achicoria” (Argentina, *Cabezas* 25, *Cabrera* 7723, 12121); “chambi” (Bolivia, *Pestalozzi* 206); “kawi kawi” (Bolivia, *Pestalozzi* 939).

Morphological characters. *Hypochaeris meyeniana* is polymorphic, with phyllaries ranging from lanceolate to ovate, generally glabrous, sometimes with shaggy trichomes. As a result of these and other morphological variations, several varieties have been described within the species. *Hypochaeris meyeniana* var. *brachylepis* was described by Cabrera (1978) to have phyllaries wider (more than 5 mm) than those normally encountered in this species. Likewise, *Hypochaeris* (as *Achyrophorus*) *meyeniana* var. *ciliata* was regarded as distinct by Weddell (1857) for plants with pubescent phyllaries. Variety *eriolaenoides* was described by Cabrera (1957) for plants characterized by deeply runcinate leaves and tomentose phyllaries. None of these features shows a consistent geographic pattern to warrant varietal status, and hence we treat *H. meyeniana* as a taxon in a broad sense.

Conservation status. Our field studies reveal that the conservation status of *Hypochaeris meyeniana* is very good. We found many and large populations, in both dry and humid rocky places in puna and prepuna (with *Trichocereus pasacana* (F. A. C. Weber) Britton & Rose, “cardon,” Cactaceae Juss.) in Jujuy Province, Argentina, and in La Paz Department, Bolivia. In Cochabamba Department, Bolivia, it occurs in *Poly-lepis tomentella* Wedd. (“tabaquillo,” Rosaceae Juss.) woods.

Observation. The type of *Achyrophorus meyenianus* was probably collected in Chile. See comments on this same locality under *Hypochaeris taraxacoides*.

Bortiri (1997) placed *Hypochaeris meyeniana* var. *ciliata* into synonymy of *H. sessiliflora*, a referral with which we do not agree. Description of “feuilles roncinées” suggests placement here in *H. meyeniana*.

Representative specimens. ARGENTINA. **Catamarca:** Andalgalá, subida al cerro Yutuyaco desde Capillitas, *Sleumer* 2730 (LP); Belén, faldeos al N de Portezuelo del río Blanco, arriba de Granadilla, *Sleumer & Vervoort* 2589 (LP, UC). **Jujuy:** Cachi, camino a Mina Don Otto, 4–5 km al S de la ruta a Cachi, *Novara* 10644 (MCNS); Cochínoca, Abra Pampa, *Vignati* 445 (LP [2], NY); Humahuaca, 20.7 km N of Humahuaca on rte. 9, *Stuessy, Urtubey & Tremetsberger* 18068 (LP [2], WU); Rinconada, Mina Pirquitas, *Schwabe, Ancibor & Vizini* 1098 (LP); Mina Aguilar, II-1968, *Fernández* 2029 (LP); entre Cachi y San Carlos, camino a Isonza, del cruce de la R 33 a la bifurcación del Santuario, *De la Fuente & Díaz* 10905 (MCNS); San Carlos, Cuesta de Isonza, 20 km S de Piedra del Molino, *Novara & Neumann* 9781 (MCNS); Susques, planicie al pie del cerro Tuzgle, *Werner* 89, 91, 103, 131 (LP); Tilcara, abra de Yala, *Fabris, Crisci & Petriella* 6514 (LP); Tumbaya, *Stuessy, Urtubey & Tremetsberger* 18062 (LP [3], WU); Valle Grande, Santa Ana, Cerro Ronque, *Kiesling et al.* 581 (LP); Yavi, Quebrada de Cajas, *Cabrera* 7826 (LP); Chalgumayoc, 15–20 km SE de Yavi, 15 km S RP 5, Km 35–38, *Tolaba, Acuña, Arapa, Gutiérrez, Quiroga, Ragno, Ramallo & da Silva* 1677 (MCNS); Abra Colorada, costados de RP 5, Km 40–45 (camino a Santa Victoria), pasando quebrada de Cajas, *Tolaba, Acuña, Arapa, Gutiérrez, Quiroga, Ragno, Ramallo & Da Silva* 1652 (MCNS). **La Rioja:** Famatina, entre Los Corrales y Cueva de Pérez, *Cabrera et al.* 27174 (SI). **Salta:** Iruya, Lomán, alrededores del pueblo de Delfina Díaz, 2 km al W de San Isidro, 14 km al NW de Iruya, *Tolaba, Ragno & Quiroga* 1235 (MCNS); Pantipampa, alrededores del puesto de Concepción Bustamante, filos del cerro al N de San Isidro, 12 km NW de Iruya, *Tolaba, Ragno & Quiroga* 1198 (MCNS); Orán, Caucillar, *Hilgert & Lamas* 1654 (MCNS); Poma, Abra Muñáño, *Cabrera* 8982 (LP); Santa Victoria, RP 7, Km 12, *Deginani, Cialdella & Bortiri* 806 (SI); Nazareno, 200 m al S del pueblo, *Adler* 2 (MCNS); San Carlos, Alturas de Amblayo, valle Isonza, 10 km S de valle Encantado, *Novara* 6356 (MCNS). BOLIVIA. **Chuquisaca:** Colomi, near Cochabamba, *Balls* 6232 (K). **Cochabamba:** Apopaya, cuenca Río Tambillo, estancia Pajchanti, *Baar* 386 (LPB); Arque, proximidades a la comunidad de Kutimarca y Sumuruni, camino hacia Arque, *Mercado* 2181 (K); Chaparre, Cerro Guakanquí, *Steinbach* 9696 (K); Cochabamba, Vacas, *Cárdenas* 4347 (US); Quillacollo, camino Sipe-Sipe-

Lipichi, *Hensen* 789 (LPB); Mizque, Sacha Ioma, *Ramírez* 203 (LPB). **La Paz:** Chaparre, about 50 km SE of Cochabamba, on rd. to Chimore, *Eyerdam* 25059 (K, UC); Ingavi, Tihuanaco, *Balls* B6361 (K, UC); Inquisivi, Cruz Sayaquira, 10 km SW of Quime, *Lewis* 37146 (US); Larecaja, ca. 23 km N of Sorata, along rd. toward Consata, *Luteyn & Dorr* 13780 (US); Los Andes, valle de Hichu Kkota, *Ostria* 132 (LPB); Murillo, La Paz, Calacoto, 60 km hacia Nevado Illimani, Panguyo, *Beck* 9060 (SI); Omasuyos, el camino principal a Peñas, 18 km via mina Fabulosa, Hichukkota, *Beck* 2861 (LPB, US); La Paz, Challapampa, *Asplund* 4886 (US); Pacajes, 39 km from La Paz along rd. to Guaqui, *King & Bishop* 7504 (US). **Oruro:** Saavedra, Kanton Amarete Felsen enmittelbar nördlich des Ortes, *Krach* 8417 (SI). **Potosí:** above presa Incachaca, 10 km from La Paz páramo, *Stuessy, Tremetsberger & Hössinger* 18504 (LP); Chayanta, Cruz Kasa, *Zamora* 156 (LPB); Frías, Potosí, “Las Lecherías,” *Schulte* 129 (LPB). **Tarija:** Aviléz, lagunas de Tajsara, *Meyer, Cuezso & Legname* 21517 (LP); Méndez, cerca Pasajes, *Bastián* 334 (US); Tarija, de Tarija a Iscayada, *Kiesling et al.* 3801, 3826 (SI). **CHILE. Región I:** Arica, camino de Arica a Portezuelo de Chapiquiña, *Ricardi, Marticorena & Matthei* 343 (CONC); Parinacota, camino entre Putre y Socoroma, Km 17, *Matthei & Rodríguez* 290 (CONC). **Región III:** Huasco, Vallenar, Río Laguna Grande, *Werdermann* 247 (LP [the label of this collection bears the herbarium name, *Hypochaeris glacialis* Weder., which was never published]). **PERU. Ancash:** Bolognesi, Ocos, *Cerrate* 6025 (SI); Huaylas, Distr. Pamparomas, Path Karka to laguna Negra Huacanam, *Weigend* 2000/615 (NY). **Arequipa:** Arequipa, Paso del Cóndor, i.e., pass on continental divide on Puno–Arequipa Rd., *Ilitis & Ugent* 1495 (US). **Ayacucho:** betw. Huanta and hacienda Pargora, *Killip & Smith* 22191 (US). **Cajamarca:** Cajamarca, entre la Encañada y Jalca de Kumulca, *López Vega* 1607 (SI); Contumazá, Cascabamba (arriba de Contumazá), *Sagástegui et al.* 10006 (US). **Huancavelica:** Castrovirreina, near Córdova, *Metcalf* 30280 (US); Huancavelica, Occopampa, entre Laria y Tambopata, a 25 km de Conaica, *Tovar* 842 (LP). **Junín:** Jauli, Anticona bajo, *Guillén & Riccio* 10784 (US). **Lima:** Canta, Ijadero, a 20 km NE de Canta, *Meza* 149 (LP); Huarochiri, Distr. San Mateo, Río Rimae, *Saunders* 822 (K). **Puno:** Huarochiri, Distr. Matucana, Km 85 on hwy., *Saunders* 379 (BM). **Tacna:** 20 km above Candasave on rd. from Mazo Cruz just S of Volcán Tutupaca, *Weigend & Förther* 97-790 (K).

7. *Hypochaeris echegarayi* Hieron., Bol. Acad. Nac. Ci. 4(1): 51. 1881. TYPE: Argentina. San Juan: Barriales de Leoncito, Dec. 1875–Jan. 1876, *D. S. Echegaray s.n.* (holotype, CORD, not located; isotype, LP!). Figure 9.

Achyrophorus setosus Wedd., Chlor. Andina 1: 220. 1857. *Hypochaeris setosa* (Wedd.) Rusby, Bull. New York Bot. Gard. 4: 402. 1907, non *Hypochaeris setosa* Formánek, 1897. TYPE: Bolivia. Potosí: “environs de Potosi,” 15–28 Mar. 1833 [Papavero, 1971], *A. C. V. D. d’Orbigny* 1425 (lectotype, designated by Cabrera [1978: 674], P!; isotypes, MO!, P!, W!).

Hypochaeris ornata J. Kost., Blumea 5(3): 660, fig. 3a, b. 1945. TYPE: Bolivia. Oruro: “am cerro de Oruro auf steinigem trockenem Boden,” 3800 m, Nov. 1911, *T. C. J. Herzog* 2522c (holotype, L, digital image!).

Hypochaeris meyeniana (Walp.) Benth. & Hook. f. ex Griseb. var. *leucantha* Cabrera, Revista Invest. Agric. 11(4):

410. 1957. TYPE: Argentina. Jujuy: Yavi, Quebrada de Cajas, 4000 m, 1 Feb. 1943, *A. L. Cabrera* 7837 (holotype, LP!).

Herbs to 5 cm tall. Leaves lanceolate or oblong, 20–70 × 3–10 mm, apex acute, base attenuate in a broad petiole, pinnatipartite to pinnatisect, runcinate, margin entire or toothed, hirsute to glabrous. Capitula pedunculate (to 2 cm), rarely sessile. Involucre campanulate, 10–25 × 8–20 mm; phyllaries 3- to 4-seriate; outer phyllaries lanceolate, 7–11 × 2–2.5 mm, apex acute or semiobtusate, hirsute on middle nerves (many to few shaggy trichomes), margin hyaline; inner phyllaries oblongate or lanceolate, 12–14 × ca. 2 mm, hirsute (shaggy trichomes) to glabrous; paleae 7–17 mm; florets 10 to 20. Corollas white, 13.5–20 mm; tube 7–10 mm; ligule 6.5–10 mm; vascularization type 1; stamens 14–17 mm; anthers ca. 5 mm; basal appendages type 2, 0.6–0.8 mm; filaments 9–12 mm; antheropodium type 1; style 12–15 mm, branches 2–3 mm. Cypselae 5-ribbed, unbeaked or slightly narrower at the apex, 2–6 mm; wall scaly or smooth; pappus 12–14 mm. Chromosome number unknown (a possible hybrid with *Hypochaeris meyeniana*, however, has been reported as $2n = 16$; Weiss-Schneeweiss et al., 2007).

Habitat and distribution. *Hypochaeris echegarayi* occurs in the mountains of Peru to northwestern-western Argentina (to San Juan Province), in bogs or dry places, 3100–4950 m (Fig. 4C, triangles).

Phenology. *Hypochaeris echegarayi* flowers from December to March.

Common name. “Q’ausilla” (Bolivia, *Petalozzi* 194).

Morphological characters. *Hypochaeris echegarayi* has shaggy trichomes on the leaves, phyllaries, and corollas. This species is closely related to *H. eremophila*, which has yellow corollas.

Observations. *Achyrophorus sessiliflorus* (Kunth) DC. var. *subruncinatus* A. Gray (1861: 146) is an illegitimate name that included both *A. setosus* Wedd. and *A. eriolaenus* Sch. Bip. as synonyms. The diagnosis by Gray (1861) corresponds more closely to the former than to the latter.

During 1874 and 1883, Hieronymus worked in the herbarium CORD of Argentina (Stafleu & Cowan, 1979), and his main collection is deposited there. In a thorough search of that herbarium, we have been unable to locate holotype material.

Cabrera (1957) originally described *Hypochaeris meyeniana* var. *leucantha* as new based on its white flowers. In 1978, he relegated this name to synonymy under *H. echegarayi* Hieron.

The small specimen of *Hypochaeris ornata*, plus the clear figure that accompanies the protologue, showing diagnostic features of campanulate involucre, setulose phyllaries, and runcinate leaves, allows referral to *H. echegarayi*. The protologue (Koster, 1945) does not mention the color of the corollas, and the colors of the specimen are faded.

Representative specimens. ARGENTINA. **Jujuy:** Cochinnoca, Mina Aguilar, Meyer, Cuezco & Legname 21305 (LP); Humahuaca, Mina Aguilar, Cabrera et al. 19002 (LP); Rinconada, Mina Pirquitas, Quebrada Cortadera, Schwabe, Ancibor & Vizini 909 (LP); Santa Catalina, ciénaga cerca de Cienaguillas, Cabrera et al. 15393 (LP, NY); Tumbaya, Abra Grande de Volcán, Sleumer 3507 (SI); Yavi, Quebrada de Cajas, Cabrera et al. 21505 (LP); alrededor de La Quica, Hunziker & Caso 6039 (LP). **San Juan:** Iglesia, Reserva San Guillermo, Los Caserones, Casal, Pujalte & Reca 17 (SI). **Tucumán:** Tafí, Cumbre de Chaquivil, Olea 241 (UC). BOLIVIA. **Cochabamba:** Tapacarí, 2 km al E de Japo K'asa (Km 125 Cochabamba–Oruro), cerro Kampiyani, Pestalozzi 194 (LPB); 42 km from Caracollo, on the rd. to Cochabamba, King & Bishop 7530 (US). **La Paz:** Aroma, Fisel U-123 (LPB); Juan Bautista Saavedra, Mergel-Kalksandstein-Hornstein-Lager, ca. 1 km S Kreuzung an der Straße nach Escoma, Krach 7672 (LP, SI); Inquisivi, Quime, 25 km hacia Caxata, Beck 17244 (LPB, US); Pedro Domingo Murillo, vic. of lago Zongo at the head of the Zongo valley, Solomon 13153 (LPB, NY); Presa Incachaca, 10 km NE from La Paz, Stuessy, Tremetsberger & Hössinger 18503 (LP); 13.4 km N of Huilacala, Stuessy, Tremetsberger & Hössinger 18515 (LP); laguna Cañuma, N.P., Stuessy, Tremetsberger & Hössinger 18516 (LP); 3 km E from Kalullo (ca. 38 km NNE from La Paz), valle de Achachicala, Stuessy, Tremetsberger & Hössinger 18525 (LP); Franz Tamayo, Puyo-Puyo (Ulla-Ulla), Menhofer X-1880 (LPB); Pacajes, entre Corocoro y Topohoco, Ceballos et al. 180 (SI). **Oruro:** Sajama, Cantón Lagunas, Loza de la Cruz 253 (LPB). **Potosí:** N de Potosí, entre Bolívar y Oruro, Fernández Casas 8025 (NY). PERU. **Lima:** Huarichori, Casapalca, Marcapomacocha rd. to Ratontay, Sanderman 853 (K). **Puno:** Puno, San Antonio de Esquilante, minas de San Antonio, Sanderman 3915 (K).

8. *Hypochaeris eremophila* Cabrera, Notas Mus. La Plata 13: 22. 1948. Replacement name for *Distoecha taraxacoides* Phil., Anales Mus. Nac. Santiago de Chile 8: 37, tab. 2, fig. 2. 1891, non *Distoecha taraxacoides* Ball, 1885. TYPE: Chile. Región III: Copiapó, Colorados [26°59'S, 68°56'W; Muñoz Pizarro, 1960: 171], 3600 m, 15 Jan. 1885, A. Philippi s.n. (lectotype, designated here, SGO 65208!, SGO photo LP!, SGO digital image!). Figure 10.

Herbs to 7 cm tall. Leaves lanceolate or obovate, 20–70 × 5–12 mm, generally deeply runcinate, glabrous or hispid principally on the midrib, base attenuate in a broad petiole, margin toothed or entire. Capitula pedunculate to 30 mm, rarely sessile. Involucre campanulate-cylindrical, 13–18 × 10–18 mm; phyllaries 3-seriate, lanceolate, apex acute, margin with shaggy trichomes to 7 mm long; outer

phyllaries 10–14 × 2.5–4 mm; inner phyllaries acute or slightly obtuse, glabrous or only slight trichomes, 14–17 × 2–3 mm; paleae 11–14 mm; florets 15 to 25. Corollas yellow to yellow-orange, 12–20 mm; tube 5–10 mm; ligule 7–10 mm; vascularization type 1; stamens 11–18 mm; anthers 5–6 mm; basal appendages type 2 or 3, 0.8–1 mm; filaments 6–12 mm; antheropodium type 1; style 10–14 mm, with branches ca. 3 mm. Cypselae 5-ribbed, transversely wrinkled, erostrate, narrowed at the apex, 2.3–4 mm; wall scaly; pappus 7–11 mm. Chromosome number $2n = 8$ (Weiss-Schneeweiss et al., 2007).

Habitat and distribution. *Hypochaeris eremophila* occurs from southern Peru to northwestern Argentina, inhabiting dry places, bogs, and “mallines,” 2800–4700 m (Fig. 4C, stars).

Phenology. *Hypochaeris eremophila* flowers from November to April.

Common names. “Achicoria” (Argentina, Cabrera 8399); “cóndor siki” (Bolivia, Meneses P602-6).

Morphological characters. *Hypochaeris eremophila* can be distinguished from the other acaulescent species of *Hypochaeris* by its peduncles with cylindric-campanulate involucre, phyllaries with shaggy trichomes on the abaxial surface, and yellow (sometimes yellow-orange) corollas.

Observation. Cabrera (1948: 22) proposed the name *Hypochaeris* [*Hypochoeris*] *eremophila* when he moved *Distoecha taraxacoides* into *Hypochaeris*, because *H. taraxacoides* Ball was already occupied. See more detailed comments under *H. taraxacoides* in this treatment.

Muñoz Pizarro (1960) listed two original specimens of *Distoecha taraxacoides* from the type locality in Philippi's herbarium at SGO. We have selected SGO65208 as lectotype because it is the better of the two specimens.

Representative specimens. ARGENTINA. **Catamarca:** Belén, camino a Antofagasta, Pasto Ventura, Cabrera, Botta & Deginani 32555 (SI). **Jujuy:** Susques, Quebrada de Tocomar, Cabrera 8278 (LP); al pie del Cerro Tuzgle, Cabrera 8399 (LP); Tumbaya, 33.3 km W of Purmamarca, Stuessy, Urtubey & Tremetsberger 18064 (LP [2]); Valle Grande, subida a cerro Amarillo desde Alto de Calilegua, Kiesling, Ulibarri & López 1720 (SI). **Salta:** Cachi, Cerro de Cachi, Spegazzini s.n. (LP); Guachipas, Pampa Grande, Spegazzini s.n. (LP); Pastos Grandes, Abra del Gallo, Cabrera 9051 (LP). **Tucumán:** Tafí, Tafí, cumbres Calchaquíes, Co. Bayo alrededores del refugio, Gómez Sosa & Múlgura 157 (SI [2]). BOLIVIA. **Cochabamba:** at Challa, on the rd. to Cochabamba, King & Bishop 7538 (US). CHILE. **Región II:** Loa, Collahuasi, quebrada Capella, Pisano & Venturelli 1726 (LP). PERU. **Puno:** Grau, Chuquibambilla, Pennell 13362 (US).

9. *Hypochaeris acaulis* (J. Rémy) Britton, Bull. Torrey Bot. Club 19: 371. 1892. Basionym:

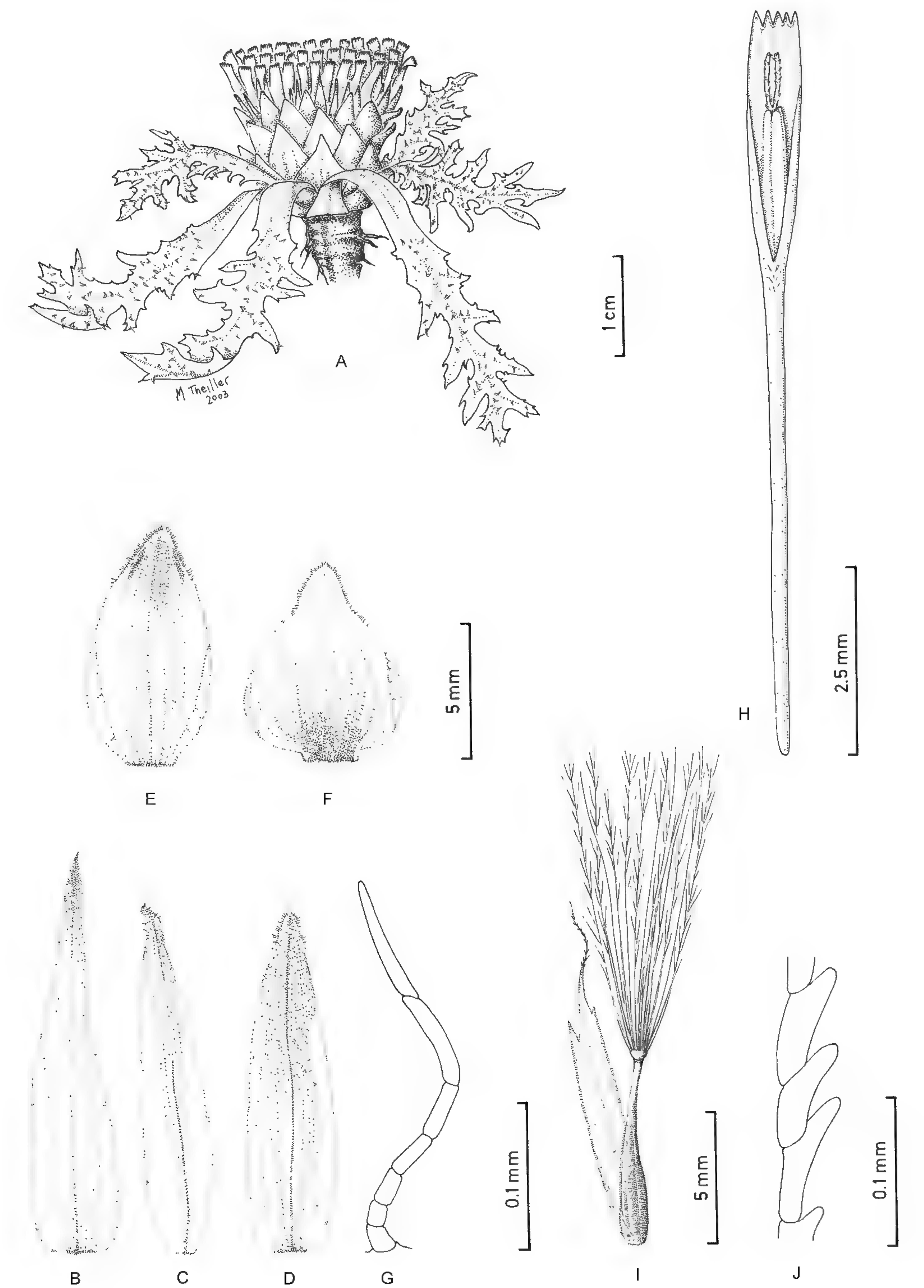


Figure 12. *Hypochaeris acaulis*. —A. Habit. —B–F. Phyllaries. —G. Trichomes (in cilia) on phyllaries. —H. Corolla with anthers and style. —I. Palea, cypselae, and pappus. —J. Scaly cypselar wall. From López 1825 (LP).

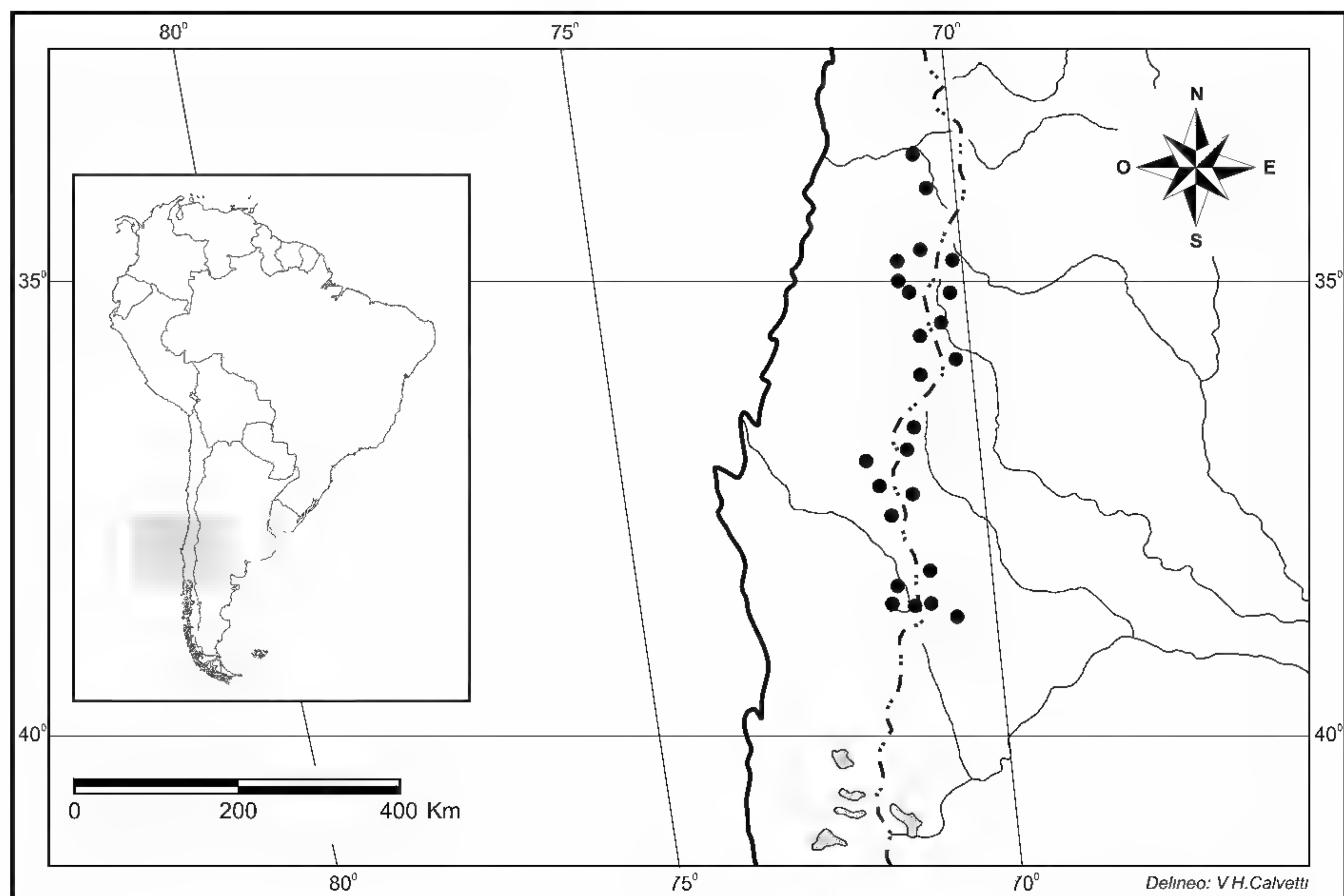


Figure 13. Distribution of *Hypochaeris acaulis* in the southern Andes (Chile and Argentina).

Achyrophorus acaulis J. Rémy, in Gay, Fl. Chil. 3: 448. 1847 [late 1848 or early 1849; Stafleu & Cowan, 1976]. TYPE: Chile. Region VI: Cachapoal, "Se cria en los prados pantanosos de las altas cordilleras de Talcaregue, provincia de Colchagua," 5–7 Feb. 1831 [Muñoz Pizarro, 1944], *C. Gay s.n.* (holotype, P not seen, P photo SI!; isotype, K!). Figure 12.

Herb to 5 cm high. Leaves oblongate, $32\text{--}60 \times 12\text{--}20$ mm, pinnatisect, with divisions antrose, base attenuate in a broad petiole, margin entire or toothed, with some shaggy trichomes (also on nerves) or glabrous. Capitula sessile. Involucre campanulate or hemispheric, $13\text{--}23 \times 10\text{--}25$ mm; phyllaries 4- to 6-seriate; outer phyllaries broadly ovate, $8\text{--}10 \times 6\text{--}8$ mm; inner phyllaries lanceolate, $8\text{--}15 \times 3\text{--}5$ mm, margin ciliate; paleae 13–16 mm; florets ca. 40. Corollas yellow, 10–14 mm; tube 5–6.5 mm; ligule 5–7.5 mm; vascularization type 1; stamens 7–9 mm; anthers ca. 2 mm; filaments 5–7 mm; basal appendages type 1, ca. 0.3 mm; antheropodium type 3; style 7–10 mm, with branches ca. 1.5 mm. Cypselae 5-ribbed, transversely wrinkled, 3.5–8 mm, rostrate; wall scaly; pappus 10–15 mm. Chromosome number $2n = 8$ (Wulff, 1998; Weiss et al., 2003).

Habitat and distribution. *Hypochaeris acaulis* grows only in the southern Andean Cordillera across a range about 600×150 km, from the regions of Santiago Metropolitan to Araucanía of Chile and provinces of Mendoza to Neuquén of Argentina (Fig. 13). It occurs between 1430 and 3000 m in

bogs, marshy places, humid meadows, stream banks, and *Araucaria araucana* (Molina) C. Koch woods. It also can be found occasionally in disturbed areas near roads and buildings.

Phenology. *Hypochaeris acaulis* flowers from December to March.

Morphological characters. *Hypochaeris acaulis* can be clearly distinguished from the other acaulescent species of the genus by its widely ovate outer phyllaries, yellow corollas slightly longer than the involucre, and the long rostrate cypselae. Tremetsberger et al. (2003a) have completed a molecular (AFLP) study of seven populations of *H. acaulis* from Chile and Argentina. All data point to restricted gene flow among populations, probably due to limited dispersal capability. There is also the expected positive correlation between genetic variation and population size. The species is postulated to be inbreeding (autogamous), based on pollen:ovule ratios, which would be consistent with the observed pattern of genetic variation. Based on other AFLP data (Tremetsberger et al., 2006), the evolutionary relationships of this taxon appear to reside with *H. palustris* and *H. tenuifolia* and not with the other acaulescent members of the South American species of the genus. This appears to be a rather dramatic case of parallelism of morphological features for survival in the high Andes.

Representative specimens. ARGENTINA. **Mendoza:** Malargüe, Paso Pehuenche, sobre la frontera con Chile, Boelcke, Bacigalupo & Correa 10379 (LP, SI). **Neuquén:** Minas, extremo S laguna Varvarco Campos, cajón del Varvarco,

Boelcke et al. 14111 (LP, SI); Ñorquín, Copahue, *Cabrera 1440* (LP); Termas de Copahue, *Cabrera 6154* (LP [2]); Picunches, ca. 1 km down from Pino Hachado, small laguna, *Stuessy & Baeza 15593* (CONC, WU); Zapala, *Comber 1257* (K). CHILE. **Región VI:** Cachapoal, Rancagua, Cordillera de Codegua, *Barros 3790* (LP). **Región VII:** Curicó, Cordillera Volcán Peteroa, *Wedermann 610* (BM, K, LP [2], SI, UC); Talca, laguna de Maule, *Stuessy & Baeza 15571* (CONC, WU); Alto de Vilches, camino a laguna El Alto, *Finot & López 1825* (CONC). **Región VIII:** Ñuble, valle de Las Nieblas (near Termas de Chillán), *Stuessy & Baeza 15565* (CONC, WU); Bio-Bio, Los Barros, ca. 1 km N of reten de carabineros, *Stuessy & Baeza 15703* (CONC, WU). **Región IX:** Malleco, below volcán Tolhuaca, *Stuessy & Baeza 15817* (CONC, WU); Cautín, Cordillera Las Raíces, Lonquimay, *Burkart 9528* (SI). **Región Metropolitana:** Santiago, Valle Largo, (Mapochotal) bei Las Condes Hochkordillera, *C. & G. Grandjot s.n.* (LP).

Literature Cited

- Babcock, E. B. 1947. The genus *Crepis*. Part two. Systematic treatment. Univ. Calif. Publ. Bot. 22: 199–1030.
- Baeza, C. M., J. Grau, E. Vosyka, T. F. Stuessy & H. Weiss. 2000. Recuentos cromosómicos en especies de *Hypochaeris* L. (Asteraceae) de Chile. Gayana, Bot. 57: 105–106.
- Bentham, G. & J. D. Hooker. 1873. *Hypochaeris*. Pp. 519–520 in G. Bentham & J. D. Hooker (editors), *Genera Plantarum*, Vol. 2. Reeve & Co., London.
- Bortiri, E. 1997. Novedades en *Hypochoeris* (Compositae, Cichorieae) de la Argentina. Hickenia 2: 223–232.
- . 1999. 280. Asteraceae, parte 14. Tribu XIII. Lactuceae: *Hypochoeris*. Pp. 3–25 in L. A. Espinosa (coordinator), *Flora Fanerogámica Argentina*, Fasc. 63. Programa PROFLOA (CONICET), Córdoba.
- Cabrera, A. L. 1948. Compuestas nuevas del noroeste de la Argentina. Notas Mus. La Plata 13: 7–23.
- . 1957. La vegetación de la República Argentina. VI. La vegetación de la Puna Argentina. Revista Invest. Agric. 11: 317–412.
- . 1978. *Hypochaeris*. Pp. 671–677 in A. L. Cabrera (editor), *Flora de La Provincia de Jujuy*, Parte X. Compositae. INTA, Buenos Aires.
- Cuatrecasas, J. 1964. Studies on Andean Compositae: VI. Proc. Biol. Soc. Wash. 77: 127–156.
- Diers, L. 1961. Der Anteil an Polyploiden in den Vegetationsgürteln der westkordillere Perus. Z. Bot. 49: 437–488.
- Division of Geography (Department of the Interior). 1955. NIS Gazeteer: Bolivia. Central Intelligence Agency, Washington, D.C.
- Enock, C. R. 1908. Peru: Its Former and Present Civilisation, History and Existing Conditions, Topography and Natural Resources, Commerce and General Development. T. Fisher Unwin, London.
- Fuchs, C. 1963. Fuchsin staining with NaOH clearing for lignified elements of whole plants or plant organs. Stain Technol. 38: 141–144.
- Goloboff, P. A. 1998. Pee-Wee, ver. 3, program and documentation. Willi Hennig Society web site. <<http://www.cladistics.org/education.html>>, accessed 2 September 2009.
- Gray, A. 1861. Characters of some Compositae in the collection of the United States South Pacific Exploring Expedition under Capt. Wilkes; with observations, etc. Proc. Amer. Acad. Arts 5: 114–146.
- Harris, J. G. & M. W. Harris. 1994. Plant Identification Terminology: An Illustrated Glossary. Spring Lake Publishing, Spring Lake, Utah.
- Herzog, T. 1923. Die Pflanzenwelt der bolivischen Anden und ihres östlichen Vorlandes. Wilhelm Engelmann, Leipzig.
- Hieronymus, G. 1896. Plantae Stuebelianae novae. Engl. Bot. Jahrb. Syst. 21: 306–378.
- Hoffmann, O. 1893. *Hypochaeris*. Pp. 361–363 in A. Engler & E. Prantl (editors), *Die natürlichen Pflanzenfamilien*, vol. 4 (5). Wilhelm Engelmann, Leipzig.
- Jansen, R. K. & T. F. Stuessy. 1980. Chromosome counts of Compositae from Latin America. Amer. J. Bot. 67: 585–594.
- Koster, J. T. 1945. Plantae a Th. Herzogio initinere eius Boliviensi altero annis 1910 et 1911 collectae, Compositae, Cichorieae. Blumea 5: 659–661.
- Kunth, C. S. 1818. Compositae: *Hypochaeris*. Pp. 1–2 in F. Humboldt, A. Bonpland & C. S. Kunth (editors), *Nova Genera et Species Plantarum* (quarto ed.) 2. Sumptibus Librariae Graeco-Latino-Germanicae, Paris.
- Kuntze, O. 1898. Revisio Generum Plantarum, Pt. 3(2). Arthur Felix, Leipzig.
- McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema & N. J. Turland (editors). 2006. International Code of Botanical Nomenclature (Vienna Code). Regnum Veg. 146.
- Metcalf, C. R. & L. Chalk. 1950. Anatomy of the Dicotyledons, Vols. 1 and 2. Clarendon Press, Oxford.
- & ———. 1979. Anatomy of the Dicotyledons, ed. 2, Vol. 1. Clarendon Press, Oxford.
- Moench, C. 1802. Supplementum ad Methodum Plantas. Marburgi Cattorum.
- Morrain, S. A. 1984. Systematic and Regional Biogeography. Van Nostrand Reinhold Company, New York.
- Muellner, A. N., K. Tremetsberger, T. Stuessy & C. M. Baeza. 2005. Pleistocene refugia and recolonization routes in the southern Andes: Insights from *Hypochaeris palustris* (Asteraceae, Lactuceae). Molec. Ecol. 14: 203–212.
- Muñoz Pizarro, C. 1944. El itinerario de don Claudio Gay. Bol. Mus. Nac. Hist. Nat. 22: 27–44.
- . 1960. Las Especies de Plantas Descritas por R. A. Philippi en el Siglo XIX. Universidad de Chile, Santiago.
- Nixon, K. C. 1999. Winclada, ver. 0.99+ (BETA). <<http://www.cladistics.com>>, accessed 2 September 2009.
- Olsen, J. 1980. In Chromosome number reports LXVII. Taxon 29: 347–367.
- Papavero, N. 1971. Essays on the History of Neotropical Dipterology, with Special Reference to Collectors (1750–1905). Museu de Zoologia, Universidade de São Paulo, São Paulo.
- Parker, J. S. 1971. The Control of Recombination. Ph.D. Thesis, University of Oxford, Oxford.
- Ratzeburg, J. T. C. 1843. Meyen's Lebenslauf. Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(suppl. 1): xiii–xxxii.
- Reiche, K. 1905. Estudios críticos sobre la flora de Chile. Anal. Univ. Chile 116: 575–606.
- Samuel, R., T. F. Stuessy, K. Tremetsberger, C. M. Baeza & S. Siljak-Yakovlev. 2003. Phylogenetic relationships among species of *Hypochaeris* (Asteraceae, Cichorieae) based on ITS, plastid *trnL* intron, *trnL-F* spacer, and *matK* sequences. Amer. J. Bot. 90: 496–507.
- Sandwith, N. Y. 1926. Humboldt and Bonpland's itinerary in Ecuador and Peru. Kew Bull. 1926: 181–190.
- Schultz Bipontinus, C. H. 1845. Hypochoerideae. Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 21: 86–172.

- . 1855. Lechler's *Plantae Peruviana*. Bonplandia 3: 236.
- . 1856. Lechler's neueste Sammlungen aus Peru und Chile. Bonplandia 4: 50–54.
- . 1859. Revisio critica generis *Achyrophori*. Pollichia 16–17: 45–73.
- Stafleu, F. A. & R. S. Cowan. 1976. Taxonomic Literature, ed. 2, Vol. 1: A–G. Bohn, Scheltema & Holkema, Utrecht.
- & ———. 1979. Taxonomic Literature, ed. 2, vol. 2: H–L. Bohn, Scheltema & Holkema, Utrecht.
- & ———. 1981. Taxonomic Literature, ed. 2, vol. 3: Lh–O. Bohn, Scheltema & Holkema, Utrecht; W. Junk, The Hague.
- & ———. 1988. Taxonomic Literature, ed. 2, vol. 7: W–Z. Bohn, Scheltema & Holkema, Utrecht; W. Junk, The Hague.
- Steudel, E. G. 1841. Nomenclator Botanicus, ed. 2, Vol. 2. J. G. Cotta, Stuttgart.
- Taylor, D. W. 1991. Paleobiogeographic relationships of Andean angiosperms of Cretaceous to Pliocene age. Paleogeogr. Paleoclimatol. Palaeoecol. 88: 69–84.
- Tremetsberger, K., T. F. Stuessy, Y.-P. Guo, C. M. Baeza, H. Weiss & R. M. Samuel. 2003a. Amplified fragment length polymorphism (AFLP) variation within and among populations of *Hypochaeris acaulis* (Asteraceae) of Andean southern South America. Taxon 52: 237–245.
- , ———, R. M. Samuel, C. M. Baeza & M. F. Fay. 2003b. Genetics of colonization in *Hypochaeris tenuifolia* (Asteraceae, Lactuceae) on Volcán Lonquimay, Chile. Molec. Ecol. 12: 2649–2659.
- , H. Weiss-Schneeweiss, T. Stuessy, R. Samuel, G. Kadlec, M. A. Ortiz & S. Talavera. 2005. Nuclear ribosomal DNA and karyotypes indicate a NW African origin of South American *Hypochaeris* (Asteraceae, Cichorieae). Molec. Phylogen. Evol. 35: 102–116.
- , T. F. Stuessy, G. Kadlec, E. Urtubey, C. M. Baeza, S. G. Beck, H. A. Valdebenito, C. de Fátima Ruas & N. I. Matzenbacher. 2006. AFLP phylogeny of South American species of *Hypochaeris* (Asteraceae, Lactuceae). Syst. Bot. 31: 610–626.
- Uphof, J. C. 1962. Pflanzenhaare, Vol. 4(5). Pp. 1–206 in K. Linsbauer (editor), Handbüch der Pflanzenanatomie. Gebrüder Borntraeger, Berlin.
- Walpers, W. G. 1846. Repertorium Botanices Systematicae, Vol. 6(2). F. Hofmeister, Leipzig.
- Weddell, H. A. 1857. Chloris Andina, Vol. 1, Pt. 7. P. Bertrand, Paris.
- Weiss, H., T. F. Stuessy, J. Grau & C. Baeza. 2003. Chromosome reports from South American *Hypochaeris* (Asteraceae). Ann. Missouri Bot. Gard. 90: 56–63.
- Weiss-Schneeweiss, H., T. F. Stuessy, S. Siljak-Yakovlev, C. M. Baeza & J. Parker. 2003. Karyotype evolution in South American species of *Hypochaeris* (Asteraceae, Lactuceae). Pl. Syst. Evol. 241: 171–184.
- , T. F. Stuessy, K. Tremetsberger, E. Urtubey, H. Valdebenito, S. Beck & C. M. Baeza. 2007. Chromosome numbers and karyotypes of South American species and populations of *Hypochaeris* (Asteraceae). Bot. J. Linn. Soc. 153: 49–60.
- , K. Tremetsberger, G. M. Schneeweiss, J. S. Parker & T. F. Stuessy. 2008. Karyotype diversification and evolution in diploid and polyploid South American *Hypochaeris* (Asteraceae) inferred from rDNA localization and genetic fingerprint data. Ann. Bot. 101: 909–918.
- Wulff, A. F. 1998. Estudios cariológicos en Asteraceae. VIII. Darwiniana 35: 37–43.

APPENDIX 1. Morphological characters and character states used for cladistic analysis of the *Hypochaeris sessiliflora* complex. See also Figure 1.

1. **Habit:** caulescent or peduncle longer than leaves (0); acaulescent or peduncle never longer than the leaves (1).
2. **Stem:** simple or bifurcating (0); ramified (1).
3. **Leaf shape:** lanceolate (0); linear (1); obovate (2); elliptic (3); linear-lanceolate (4); linear-filiform (5).
4. **Leaf margin:** dentate (0); entire (1); divided (2).
5. **Leaf vestiture:** shaggy (0); whip (1); shaggy and whip (2); glabrous (3).
6. **Involucre:** campanulate (0); hemispheric (1); cylindric (2); cylindric-campanulate (3).
7. **Capitulum:** pedunculate (0); sessile (1).
8. **External phyllary shape:** linear-lanceolate (0); lanceolate (1); ovate (2).
9. **Phyllary vestiture (abaxial):** whip and shaggy trichomes (0); whip trichomes (1); shaggy trichomes (2); absent (3).
10. **Length of corolla:** longer than the involucre (0); as long as involucre (1).
11. **Corolla vascularization:** type 2 (0); type 1 (1).
12. **Basal appendages:** type 2 (0); type 1 (1); type 3 (2).
13. **Antheropodium:** type 1 (0); type 3 (1); type 2 (2).
14. **Cypselar shape:** rostrate (0); semirostrate (1); erostrate (2).
15. **Cypselar wall:** scaly on all surfaces (0); smooth (1); scaly on main portion only (2).
16. **Palea surface:** pubescent (0); glabrous (1).

APPENDIX 2. Data matrix used in the cladistic analysis of the *Hypochaeris sessiliflora* complex. Dashes indicate missing data or inapplicable states.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Outgroup																
<i>H. argentina</i>	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
<i>H. caespitosa</i>	0	–	4	01	3	0	0	0	1	0	1	0	1	1	1	0
<i>H. chillensis</i>	0	1	0	02	13	3	0	0	013	1	1	1	1	0	0	0
<i>H. elata</i>	0	01	0	0	3	0	0	0	0	1	1	0	1	0	0	0
<i>H. hookeri</i>	1	–	5	01	13	3	0	0	1	0	1	1	0	2	1	0
Ingroup																
<i>H. acaulis</i>	1	–	1	2	03	01	1	2	3	0	1	1	1	0	2	1
<i>H. echegarayi</i>	1	–	01	2	03	0	01	1	2	0	1	0	0	12	01	1
<i>H. eremophila</i>	1	–	02	02	03	3	01	1	2	0	1	02	0	02	0	1
<i>H. eriolaena</i>	1	–	01	01	013	01	1	12	1	0	0	01	02	12	0	1
<i>H. hohenackeri</i>	1	–	1	01	3	0	0	1	3	0	1	01	02	2	1	1
<i>H. meyeniana</i>	1	–	023	2	03	01	01	12	123	0	01	02	0	1	01	1
<i>H. mucida</i>	1	–	1	02	2	0	1	1	0	0	1	1	0	2	1	1
<i>H. sessiliflora</i>	1	–	34	0	3	01	01	012	23	0	1	02	02	12	01	1
<i>H. taraxacoides</i>	1	–	01	02	3	2	0	0	3	0	0	2	0	2	1	1

- APPENDIX 3. Vouchers for the cladistic analysis.
- Outgroup**
Hypochaeris argentina: Burkart et al. 10486 (LP); Krapovichkas 7806 (LP); Urtubey & Tremetsberger 146 (LP, WU)
H. caespitosa: Castellanos s.n. (LP); Hunziker 8649 (LP); Urtubey & Tremetsberger 145 (LP, WU)
H. chillensis: Cabrera 5688, 8595 (LP); Urtubey & Tremetsberger 114 (LP)
H. elata: Cabrera et al. 16971, 17657 (LP); Stuessy et al. 18080, 18083 (LP, WU)
H. hookeri: Stuessy et al. 18019, 18044 (LP)
Ingroup
H. acaulis: Boelcke et al. 10379 (LP); Cabrera 6154 (LP); López 1825 (LP)
H. echegarayi: Hunziker & Caso 6039 (LP); Cabrera et al. 15393 (LP); Meyer, Cuezso & Legname 21305 (LP); Stuessy et al. 18025 (LP)
H. eremophila: Burkart 5234 (LP); Cabrera 8278, 8399 (LP); Stuessy et al. 18064 (LP)
H. eriolaena: Angulo & López 1358 (LP); Hutchison, Wright & Straw 6267 (US); Macbride & Featherstone 2487 (LP, US); Velarde Núñez 3225 (LP)
H. hohenackeri: Lewis 35168 (LPB); Menhofer X-1832 (SI, LPB); Smith & Cabanillas 7212 (US).
H. meyeniana: Bundin s.n. (LP); Fabris 6514 (LP); Fernández 2029 (LP); Meyer 21270 (LP); Stuessy et al. 18062 (LP)
H. mucida: Ceballos et al. 614 (SI); Menhofer X-2197 (LPB)
H. sessiliflora: Cuatrecasas et al. 25599 (LP); Plowman 1955 (US); Molina & Barclay 18S388 (US); Stuessy et al. 18538 (WU)
H. taraxacoides: Meyer et al. 21040 (LP); Stuessy et al. 18074, 18075 (LP)

3. *Hypochaeris hohenackeri* (Sch. Bip.) Domke
4. *Hypochaeris mucida* Domke
5. *Hypochaeris eriolaena* (Sch. Bip.) Reiche
6. *Hypochaeris meyeniana* (Walp.) Benth. & Hook. f. ex Griseb.
7. *Hypochaeris echegarayi* Hieron.
8. *Hypochaeris eremophila* Cabrera
9. *Hypochaeris acaulis* (J. Rémy) Britton

Adler 2 (6); Angulo & López 1358 (5); Aristeguieta 2438 (1); Asplund 4886 (6). Baar 386 (6); Balls 6232 (6), B-6253 (2), B-6361 (6), B-6711 (2); Barclay & Juajibioy 7642 (2), 8472, 9210 (1); Barros 3790 (9); Bastián 334 (6); Beck 2861 (6), 7712 (2), 8356 (1), 9060 (6), 11914 (5), 17244 (7); Beck & Paniagua 27086 (2); Becker et Terrones 1433 (5); Blair 636 (2); Boecke & Jaramillo 2348, 2493 (1); Boelcke et al. 10379, 14111 (9); Bundin s.n. (6); Burkart 5234 (8), 9528 (9); Burkart & Troncoso 11822 (2). Cabezas 25 (6); Cabrera 1440, 6154 (9), 7723, 7826 (6), 8278, 8399 (8), 8982 (6), 8993 (2), 9051 (8), 12121 (6); Cabrera et al. 15256 (2), 15393 (7), 17656 (2), 19002 (7), 21505 (7), 22484, 22531 (2), 27174 (6), 32555 (8); Canne & Schunke 232 (5); Cárdenas 4347 (6); Casal et al. 17 (7); Ceballos et al. 164 (2), 180 (7), 548 (2), 614 (4); Cerrate 6025 (6); Cerrate & Tovar 1174 (2); Comber 1257 (9); Cuatrecasas 1484 (1); Cuatrecasas & Romero Castaneda 24560 (1); Cuatrecasas & Willard 26299 (1). Deginani et al. 806 (6); de la Fuente & Díaz 10905 (6). Ellemann 91672 (1); Ellenberg 638 (4); Eyerdam 24839 (3), 25059 (6); Ewan 16324 (1). Fabris 1369 (8), 1520 (2); Fabris et al. 4035 (2), 6514 (6); Fernández 2029 (6); Fernández Casas 8025 (7); Fiebrig 3188 (2); Finot & López 1825 (9); Fisel U-123 (7); Freueler 4384 (2). Gómez Sosa & Múlgura 157 (8); Grandjot, C. & Grandjot, G. s.n. (9); Guillén & Riccio 10784 (6). Haber 5, 142 (2); Hawkes et al. 3900 (2); Hensen 789 (6); Hilgert & Lamas 1654 (6); Hoogle & Roesch 2534 (2); J. H. Hunziker & Caso 6039 (7); Hutchison et al. 5892 (2), 6267 (5). Ibish & Rojas 439 (5); Iltis & Ugent 1256, 1489 (2), 1495 (6). Jahn 146 (1). Kiesling et al. 581 (6), 1720 (8), 3801, 3826 (6); Killip & Smith 17641, 21680 (1), 22191 (6), 23369 (1); King & Bishop 7504 (6), 7530 (7), 7538 (8); King & Collins 9064 (2); King & Garvey 6968 (1); Krach 7492 (2),

7672 (7), 8417 (6), 8435, 8672 (2), 9391 (2); Krapovickas 3155 (2). Leiteyn et al. 4995 (1); Lewis 35168 (3), 37146 (6), 38124 (3); Liberman 2343 (2); López & Sagástegui 2888, 3223, 8245 (2); López et al. 7421 (5); López Vega 1607 (6); Loza de la Cruz 72 (2), 253 (7), 254 (2); Luteyn & Dorr 13780 (6). Macbride & Featherstone 1791 (1), 2167 (2), 2487 (5); Maguire 39405 (1); Mandon 276 (2); Marticorena & Matthei 343 (6); Mathei & Rodríguez 290 (6); Meneses P602-6 (8); Menhofer 1036 (2), 1600 (2), X-1880 (7), X-1832 (3), X-2197 (4); Mercado 2181 (6); Metcalf 30280 (6); Meyer 21270 (6); Meyer et al. 21040 (2), 21305 (7), 21517 (6); Meza 149 (6), 207, 209 (5); Mezar 162 (2); Molina & Barkley 18 S.338 (1); Müller & Heinrichs 6428 (3); Müsch 151 (p.p.) (1). Novara 6356, 10644 (6); Novara & Neumann 9781 (6). Ochoa 264 (2); Olea 241 (7); Ostria 132 (6). Pennell 13362 (8); Peñafiel et al. 382 (1); Pestalozzi 194 (7), 206 (6), 284 (2), 292 (6), 606 (5), 939 (6); Pisano & Venturelli 1726 (8); Plowman 1955 (1). Ramírez 203 (6); Ricardi et al. 343 (6); Rohweder T-12 (2). Sagástegui et al. 9006 (5), 10006 (6); Sanderman 853, 3915 (7); Saunders 379, 822 (6), 1106 (2); Schulte 9 (2), 129 (6); Schwabe et al. 641 (2), 818, 819 (2), 909 (7), 1098 (6); Sleumer 2730 (6), 3507 (7); Sleumer & Vervoorst 2589 (6); Smith & Buddensiek 11133 (5); Smith & Cabanillas 7212 (3), 7328 (1); Smith et al. 5652 (2); Soejarto 494 (1); Soderstrom 1254 (1); Solomon 13153 (7), 13177 (2); Solomon & Nee 14233 (2); Spegazzini s.n., s.n. (8); Stafford 865 (5); Steinbach 9696 (6); Steyermark et al. 101105 (1); Stork & Horton 10000 (5), 10838 (2); Stuessy & Baeza 15565, 15571, 15593, 15703, 15817 (9); Stuessy et al. 18062 (6), 18064 (8), 18068 (6), 18074, 18075 (2), 18089 (2), 18503 (7), 18504 (6), 18515, 18516, 18525 (7), 18538, 18540, 18549 (1). Tolaba et al. 1198, 1235 (6), 1539 (2), 1652, 1677 (6); Tovar 222 (3), 390, 393 (2), 842 (6), 850 (2), 2512 (5); Tutin 1209, 1210 (5). Vargas 11355, 11350 (p.p.) (5), 21784 (1); Vargas et al. 2619, 2887 (1); Velarde Núñez 3225 (5); Vignati 445 (6). Wedermann 247 (6), 610 (9); Weigend 2000/615 (6), 2000/616 (1); Weigend & Forther 97-790 (6); Werner 89, 91, 103, 131 (6), 820 (2); West 3663 (2); Wevi 129 (5); Wurdack 761 (1), 1225 (3). Zamalloa Díaz 78 (2); Zamora 156 (6); Zuloaga & Landon 4136 (1).